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Damage to the Seed of Douglas-Fir by the Douglas-Fir Cone Midge

BY
NORMAN E. JOHNSON
H. J. HEIKKENEN

SERIOUS DAMAGE to the seed of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is caused by the larvae of the gall-forming midge, *Contarinia oregonensis* Foote. This insect, which will be referred to as the Douglas-fir cone midge, destroyed nearly 50 percent of the 1957 Douglas-fir seed crop in certain areas of the Pacific Northwest. The Douglas-fir cone midge accounted for damage exceeding that by all other cone-infesting insects in western Washington during the period 1955-57 (Johnson, 1958). The total cone and seed insect damage can reach such proportions as to represent a limiting factor in the production of Douglas-fir seed.

The objectives of this study were: (1) To establish the identity of the Itonidid larva causing serious damage to the seed of Douglas-fir, (2) to gather basic facts on its biology, (3) to characterize the damage caused to the cone and seed, (4) to test a method for sampling the amount of damaged seed by means of observations on an axial slice of the cone, and (5) to determine the amount of damage occurring on Weyerhaeuser Timber Company tree farms in western Washington and Oregon. This study on the Douglas-fir cone midge is part of a continuing research project on the cone and seed insects of Douglas-fir.

The association of midges (Itonididae) with Douglas-fir cones has been recognized for a long time. Miller (1914) found the larvae of "gnats or midges" in the cones of nearly all western conifers. He reported that the larvae cause small masses of resin among the scales without affecting the seed seriously. Keen (1952) noted that the larvae of gall midges may cause hard resinous galls to form on the cone scales or in the seeds, but that the damage from these insects is usually insignificant. Rudinsky (1955), indicated that in western Washington, cone gall midges were common in Douglas-fir cones but rarely destroyed the seed. Gall midges have been reported by Trip and Hedlin (1956) to cause damage to seed of white spruce (*Picea glauca* (Moench) Voss). Gäbler (1954) listed eight species of Itonididae infesting cones of *Picea*, *Pinus*, *Larix*, and *Abies* in

The authors, Forest Entomologist, and former Research Assistant, respectively, Weyerhaeuser Timber Company, Forestry Research Center, express appreciation for critical reviews to W. H. Cummings, Forestry Research Supervisor, F. P. Keen, entomologist, California Forest and Range Experiment Station, and Alan Hedlin, entomologist, Forest Biology Division, Canada Department of Agriculture. We also express thanks to Dr. R. H. Foote of the U. S. National Museum for identification of the insect, and to forestry personnel of Weyerhaeuser Timber Company for collecting the cones in this study.

Europe. He reported as high as 83 percent of *Abies* seed destroyed by the fir seed gall midge in certain areas. Foote (1956) has described the adult midges associated with cones of western conifers. *Contarinia oregonensis* was one of seven newly described species, of which four were reported to attack Douglas-fir cones. Descriptions of the immature stages of these species are not available and little is known of their biologies. Felt (1925) summarizes the general biology of the Itonididae and presents keys for the adults of many species of this large and diversified family of insects.

Description of Insect

In order to identify the species of gall-forming midge causing damage to Douglas-fir seed, it was necessary to isolate larvae from the galled cones and rear them to the adult stage. An effective rearing method was to place the larvae between moist cotton in screen-bottom containers placed in a sand table. Larvae were obtained from infested Douglas-fir cones collected in 1956 near Yacolt and Elma, Washington, and from 1957 cones collected in eight areas in western Washington and Oregon. The adults that emerged were identified by R. H. Foote of the United States National Museum as *Contarinia oregonensis* Foote. The general descriptions of the various stages presented here, along with the illustrations in Figure 1, should serve to distinguish this species from others occurring in Douglas-fir cones. Drawings were made from fresh specimens using magnification up to 54 ×. Biological information is based on periodic observations made in southwestern Washington.

Egg. In shape, the egg is oblong — approximately 260 μ in length and 80 μ in width. The chorion is smooth and shiny. When fresh, the egg is white and translucent, but after a time numerous fat bodies appear inside and impart an orange color to the egg. Some of these fat bodies become aligned longitudinally in two rows along the sides of the egg. Just prior to hatching, the larva is discernible within the egg (Fig. 1A).

Larva. When newly hatched, the larva is about 0.25 mm. long and white except for a large orange-pink group of fat bodies located just posterior to the middle. The body is somewhat flattened dorsoventrally and composed of 13 distinct body segments and a small retractible head. The spiracles on the twelfth segment are raised conspicuously. The mature larva is 3 to 4 mm. long and usually orange-pink, although white and orange specimens are encountered occasionally. The spiracles on the twelfth segment are less apparent than in the newly hatched larva. The integument is transparent and smooth except for the anterior ventral folds of segments 3 to 12 which show fine transverse striations. On the ventral surface of the second segment of the mature larva is a sclerotized forked breastplate and on the last segment is a pair of sclerotized, slightly recurved processes. The breastplate has taxonomic value, serving to separate this species from the other species of Itonididae inhabiting Douglas-fir cones. Dimensions of the breastplate of 20 mature larvae show the following averages and standard deviations: length, 233 $\pm$ 19 μ; width at anterior end, 64 $\pm$ 6 μ; width of posterior end, 41 $\pm$ 5 μ; depth of notch, 22 $\pm$ 3 μ (Fig. 1B).

Pupa. Usually the pupa is slightly shorter than the larva. At first it is orange-pink; as it matures, the legs and wings turn black, due mostly to the black hairs developing on the appendages. In the mature pupa, adult characteristics are visible through the transparent pupal skin and sex is distinguished readily. Three pairs of appendages, the thoracic horns, antennal horns, and the cephalic setae are of taxonomic importance on the pupa. The thoracic horns are acuminate, slightly curved processes, which protrude outward and forward from the prothorax. Their length is slightly greater than the distance from the base to the

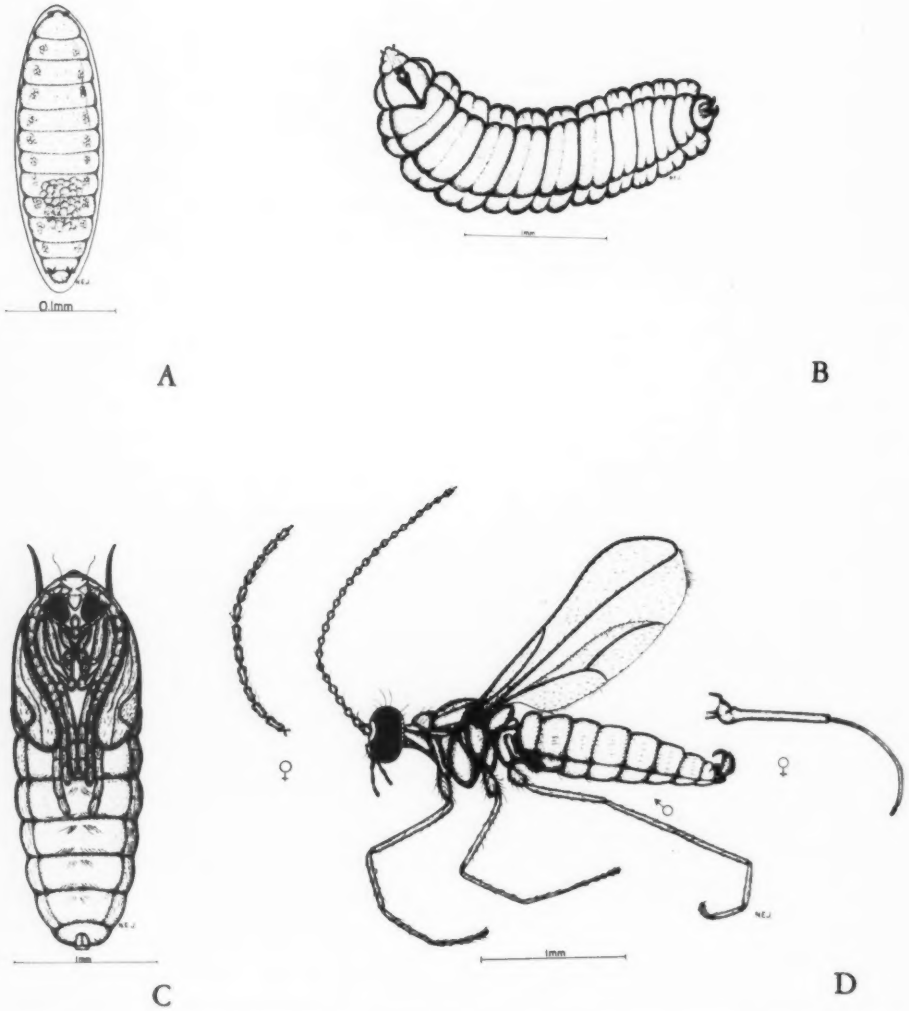

FIGURE 1. *A. Egg with larva visible through chorion. B. Mature larva, ventral view, with forked breastplate on the second segment, and posterior projections. C. Pupa (female) with prominent thoracic horns, cephalic setae, and antennal horns. D. Adult (male) with long, bead-like antennae and upturned genitalia; and contrasting female shorter antenna and ovipositor, partially extended.*

median suture of the thorax. The sclerotized antennal horns occurring at the base of the antennae, appear as irregular tetrahedrons produced to a moderately acute point. The inner edge is most heavily sclerotized. The edge projecting toward the eye terminates in a slightly raised point. In Figure 1C, the apex of the antennal horn is tilted forward for better illustration. On actual specimens, the apex projects perpendicular to the body. Directly behind the antennae is a pair of cephalic setae arising from slightly raised bases. Their length is approximately 1 1/3 times the distance between their bases.

Adult. The Douglas-fir cone midge is a delicate gnat-like insect with long legs and antennae. The wings have reduced venation, and lie flat over the abdomen when at rest. Fresh specimens have bright orange abdomens. The male is 2.3 to 2.8 mm. long with upturned genetalia. The funicle of the antenna is composed of 12 segments, each of which is deeply constricted in the middle giving the appearance of 24 separate bead-like segments (Fig. 1D). The female is 2.7 to 3.6 mm. long excluding the long retractible ovipositor, which extends to a greater length than the body. The antenna is shorter than in the male, and the 12 segments of the funicle are only slightly constricted in the middle.

Biology

The adults emerge in the spring about the time the Douglas-fir conelets are open to receive pollen. The female crawls among the bracts and with the long ovipositor selects a suitable place to oviposit, usually on the developing cone scales near the seed. The eggs may be laid singly or in clusters. Upon hatching, the larva is difficult to find in the light colored cone tissue. Feeding usually begins on or near the seed, but may be elsewhere on the cone scale. Gall formation begins soon and is evident as early as June in western Washington. The developing larva which turns pink, becomes encased in its own compartment in a single or aggregate gall. The mature larva usually leaves the Douglas-fir cone late in the fall; however, some larvae have been observed in the old cones as late as the middle of February. Like many Itonidid larvae, this species is capable of jumping action. This is accomplished by doubling the body until the posterior processes grasp in the indented segment at the base of the breastplate. Then with a rapid extension of the body the coupling loosens with a snapping motion, hurling the larva sometimes as much as a foot. Such movement helps the larvae to leave the Douglas-fir cones, since many of the cones do not fall to the forest floor until after the second or third season. The larva is capable of slow crawling movement also, especially when in contact with wet surfaces.

Upon reaching the forest floor, the larva forms an orange-brown paper-like cocoon in the litter. The larva transforms to a pupa in the spring. Pupae have been observed resting on the soil under the litter or attached to cone scales, needles, moss, or other matter. The duration of the pupal stage in the field is not known, but in the laboratory it was about two weeks. The pupa is capable of movement and pushes itself through the cocoon, the thoracic horns appearing first. It may push itself completely out of the cocoon before changing to the adult stage. The Douglas-fir cone midge is parasitized by at least one unidentified species of Chalcidoidea. In 1957, the parasitism amounted to over 40 percent in some cones.

Damage

The type of damage caused by the Douglas-fir cone midge varies with the number of larvae surrounding an individual seed and the size of the gall. When numerous larvae congregate around a seed, the aggregate gall may completely destroy and displace the seed (Figs. 2 and 3). When only a few larvae are present, the gall may not destroy the seed but fuses the seed coat

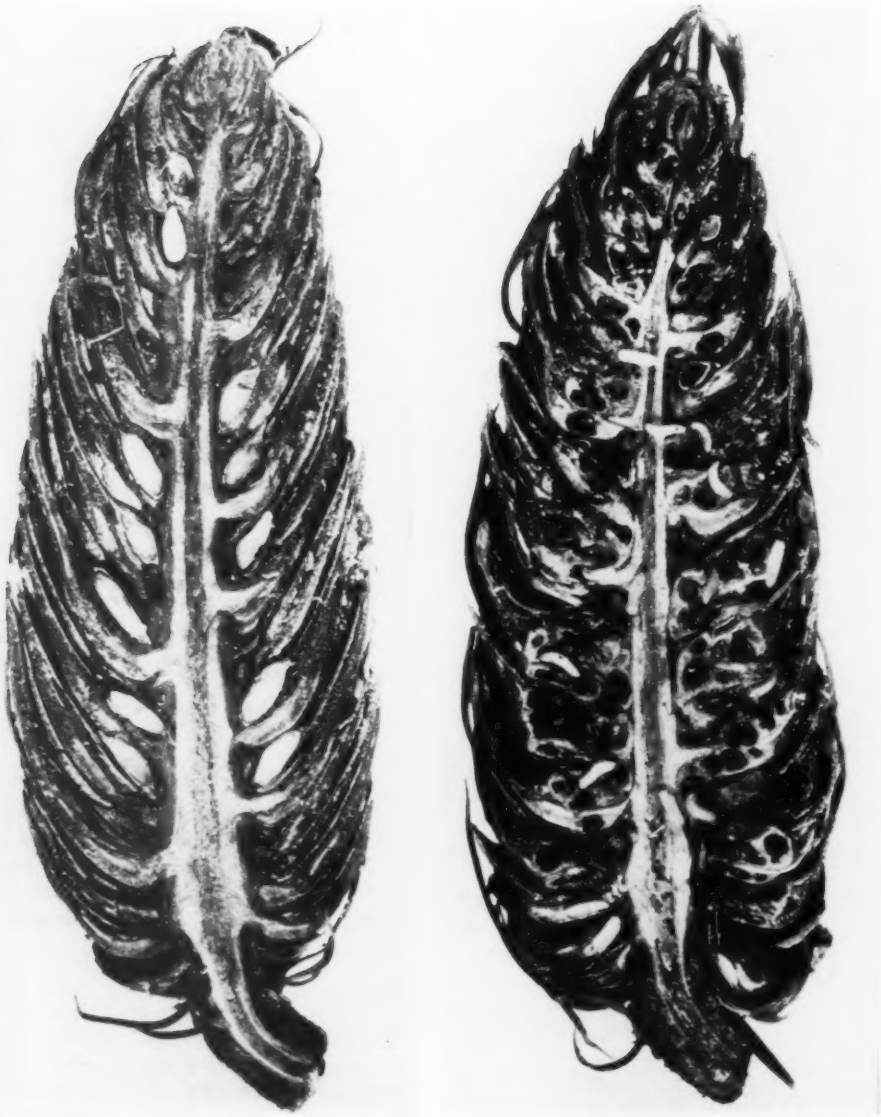

FIGURE 2. *Douglas-fir cones sectioned along axis.*
Left: Normal cone showing a filled seed count of 11.
Right: Damaged cone with numerous larvae and pock-marked appearance of the sectioned galls.

to the cone scale. Some galls may not be contiguous with the seed but may be located on the cone scale where they may fuse the seed wing to the scale tissue. The tissue comprising the gall is more dense and hard than unaffected cone tissue.

In cones with heavy infestation, the damage may be apparent externally as misshapen cone scales and occasional necrotic areas. The damage by the Douglas-fir cone midge is easily distinguished from that caused by other insects: the cone moths feed through the cone tissue destroying the seed and leaving large amounts of frass and exuding pitch. The seed chalcid (*Megastigmus spermotrophus* Wachtl.) larva occurs singly within the seed leaving no external indication of infestation. At least one other species of Itonididae among the five found during the study, may cause some damage to the seed of Douglas-fir. The larva of this unidentified species is similar to the Douglas-fir cone midge, but can be separated by morphological characteristics and type of damage. It mines within the cone scales, sometimes penetrating the seed, but does not cause a gall to form.

Before attempting an extensive sampling of the amount of damage caused by the Douglas-fir cone midge, a test was conducted to determine if galled seed would fall from the cones during processing and if the damage on an axial section of the cone was representative of damage as determined by dissection of the cone. Ten samples of 40 cones each were selected which were known to have been damaged by the Douglas-fir cone midge. Twenty cones drawn at random from each sample were sliced axially with a sharp knife (Fig. 3). Counting only those seed actually cut by the knife, the percent of seed galled by the Douglas-fir cone midge was determined.

The remaining 20 cones were dried in an oven until the cone scales reflexed, and then were tumbled in a 20-inch diameter seed-extracting cylinder for 3 minutes. The cones were then taken apart and each cone scale inspected for seed not removed during tumbling. From the count of seed extracted plus that remaining in the cones, the percent of galled seed was determined. An F

FIGURE 3. *Seed from a single damaged Douglas-fir cone. Above: Galled. Below: Normal.*

test showed no significant difference in the percent of seed damaged as determined by these two methods (Table 1). Thus, the slice test was used exclusively in further damage appraisal in place of the more time-consuming cone dissection method.

Table 1 shows the percent of galled and normal seed remaining in the cones following tumbling. This amounted to over 99 percent of the galled, empty seed and 91 percent of the galled, filled seed. This compared to 56 percent of the empty seed and 22 percent of the filled seed that had not been galled. Of the galled seed removed from the cones, more than half had seed coats broken where the seed had separated from the gall.

In order to determine the extent of damage caused by the Douglas-fir cone midge, cones were studied at varied elevations from sea level to 3,800 feet in the Douglas-fir Region of western Washington and Oregon. Samples totaling 800 green Douglas-fir cones were collected from 44 selected areas by forestry personnel of eight Weyerhaeuser Timber Company tree farms extending from Coos Bay, Oregon, to the vicinity of Everett, Washington. Each sample consisted of 20 cones, except for eight, 10-cone samples from White River Tree Farm. Cone collections were dispatched to Centralia, Washington, for intensive study. Here, the fresh cones were sliced on the axis and examined under 9 × magnification. Damage by the Douglas-fir cone midge was distinguished from that by other insects, and recorded by count of filled or empty seed.

As shown in Table 2, 13 percent of the seed of the 1957 cone crop was damaged by the Douglas-fir cone midge. There was no significant difference in midge-damage to cones collected at different elevations; however, there was a highly significant variation among tree farms. The highest was on Millicoma Forest Tree Farm where damage averaged 49 percent for five sample areas. The least amount was at White River Tree Farm where 4 percent of the seed from 11 sample areas was damaged. The overall damage by the Douglas-fir cone midge accounted for 48 percent of the total damage caused by all insects. The empty galled seed was approximately four times as great as the filled seed with galls (Table 2). This could indicate that the galling action had a detrimental effect on the developing endosperm.

Discussion

In 1955, the most abundant insect found in Douglas-fir cones collected in western Washington was the Douglas-fir cone midge (Johnson, 1956). Again in 1956, it proved the most important seed insect, destroying almost 10 percent of the seed in cones that were sampled. The results of the present study show that in 1957 the midge continues to be the most damaging insect affecting Douglas-fir cones on Weyerhaeuser Timber Company tree farms. It is possible that the Douglas-fir cone midge population in recent years was higher than average, although earlier reports indicate that midges were the most abundant insects present in cones. However, the severity of the damage caused by the midge may have been underestimated, since the results from the present study show that galled seed, even though sound, are seldom removed from the cones during seed processing. This might have been overlooked in past estimates of damage. Undoubtedly the reporting of damage has been complicated by the fact that only recently were the Itonididae affecting coniferous seed described (Foote, 1956). It appears that the Douglas-fir cone midge, among the other seed-destroying insects, can be an important factor in limiting Douglas-fir seed production.

Summary

The Douglas-fir cone midge (*Contarinia oregonensis* Foote) has caused serious losses of Douglas-fir seed in western Washington

TABLE 1. Seed remaining after extraction of midge-infested 1957 Douglas-fir cones in 10 samples of 20 cones each.

Percent of seed galled in cone sample by—		Percent of seed remaining in cone			
		Galled		Not galled	
Axial section	Total dissection	Empty seed	Filled seed	Empty seed	Filled seed
19	22	98.5	50	41	13
20	23	99.0	100	46	24
15	27	99.9	100	60	39
28	28	99.0	93	42	19
17	38	99.7	100	53	5
35	38	98.5	75	61	28
40	47	99.6	93	54	7
53	53	100.0	100	71	14
66	66	99.5	100	56	42
90	83	100.0	100	63	34
38	43	99.4	91	56	22
25	20	0.6	16	10	13

All samples:
Standard deviation:

TABLE 2. Midge-damage to 1957 Douglas-fir cones collected from sample areas on Weyerhaeuser Timber Company tree farms.

Tree farm	Number of sample areas[1]	Midge-damage percent of—			
		All seed	Filled seed	Empty seed	All insect damage
Millicoma Forest North Bend, Ore.	5	49	17	52	84
Callapooya Springfield, Ore.	1	6	0	7	82
St. Helens Longview, Wash.	6	7	1	7	22
Clemons Cosmopolis, Wash.	5	29	8	32	83
Vail-McDonald Chehalis, Wash.	7	5	1	6	49
White River Enumclaw, Wash.	11	4	0	5	29
Snoqualmie Falls Snoqualmie Falls, Wash.	4	8	0	9	56
Skykomish Monroe, Wash.	5	7	2	8	32
All areas	44	13.2	3.5	14.7	47.6
Standard deviation	....	12.4	6.3	13.2	32.4

[1]Twenty cones were collected from each area except at White River where 8 samples consisted of 10 cones each.

and Oregon during the past three years. The larva of this insect causes the plant to produce a gall around the seed in Douglas-fir cones. The galls may destroy the seed or fuse the seed coat or wing to the cone scale so that it is not removed from the cone during natural seed fall or at seed extraction plants. As much as 99 percent of galled seed may remain in the cone during processing. It was found that an accurate estimate of the percent of galled seed within a cone could be obtained from counts made on seeds exposed by slicing of cones on the axis. An appraisal made by this method on cones collected from 44 areas in western Washington and Oregon in 1957 showed that, over all, 14 percent of the seed was damaged by the Douglas-fir cone midge, and an average of 49 percent from 5 samples collected in one area.

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Natural Polyploidy in Slash Pine

BY
FRANCOIS MERGEN

In some orders, or families of plants, the chromosome number is quite variable among the different species; in others the number is quite constant. The coniferales belong in the latter group, in which polyploidy and other major chromosomal changes are rare. In the Pinaceae, particularly, all of the species studied so far occur normally as diploid plants, with the exception of *Pseudolarix amabilis* (Nehls.) Rehd. which occurs as a tetraploid. There have been several reports on the occurrence within the Pinaceae of freak plants whose chromosome number varied from that of their normal diploid ancestors. These abnormal plants were identified through their external appearance; namely, by their stunted growth, by thick fleshy needles, or by the unusual color of their foliage. There has been only one report so far of a study which verified the chromosome number of an abnormal seedling in the genus *Pinus*. The presence of polyploids, however, has been postulated by many foresters. In view of their scientific interest, and also because of their potential use as new germ plasm in tree breeding, a search was made in a forest tree nursery to locate abnormal seedlings of slash pine (*Pinus elliottii* Engelm.). The morphology of these unusual plants, along with the results of a cytological study, are reported in this paper. No review is made of polyploids that were induced by physico-chemical means; because these will be discussed in a later paper.

Review of Literature

Polyploidy is quite common in the angiosperms, in which group the general frequency of polyploid species is estimated to be about 30 to 35 percent (Stebbins, 1938). In the gymnosperms, on the other hand, polyploidy is rare. Sax and Sax (1933) reported that the golden larch, *Pseudolarix amabilis* (Nehls.) Rehd., is probably of tetraploid origin with a chromosome count of 22 in haploid tissue. A count of 44 chromosomes was obtained by the present author in the needle bases of several golden larch seedlings. Sax and Sax postulated that the current basic number of 22 chromosomes is a polyploid of an aneuploid condition with 12 chromosomes as the basic number.

To the writer's knowledge this is the only report of an autopolyploid species in the Pinaceae, but there have been occasional reports in which the occurrence of spon-

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The collection of material was started while the author was project leader of the forest tree improvement program of the Southeastern Forest Experiment Station at Lake City, Florida. Subsequent collections were made during field trips with graduate students to Lake City, Florida, under a cooperative agreement with the Southeastern Forest Experiment Station. Sincere thanks are expressed to the personnel of the Lake City Research Center, and to the Florida Board of Forestry, for allowing the collection of the material. Lola E. Koerting assisted with the laboratory work and the writer is indebted for this help. P. F. Bourdeau and H. J. Lutz critically reviewed the manuscript, and their advice was most helpful.

taneous polyploid individuals in this family were described. Most of these polyploid trees were found in nursery beds. Kanezawa (1938) located a heteroploid *Abies firma* Sieb. et Zucc. seedling which originated from a twin plant. He determined the chromosome numbers on 3 twin seedlings, and one of these was a tetraploid with 48 chromosomes. By looking for aberrant seedlings of *Picea Abies* (L.) Karst. in a total population of 1,200,000 nursery transplants, Kiellander (1950) sorted out 93 morphologic aberrants. Of these, 49 were diploids, one was triploid, 22 were tetraploids, and three were mixoploids. He was unable to determine the chromosome number of the remaining 18 seedlings. Previous to this systematic selection, Kiellander had discovered an aneuploid spruce seedling with $2n = \pm 28$ chromosomes. Christiansen (1950) located a large tetraploid *Larix decidua* Mill. tree in Denmark which he considered to be autotetraploid. Chiba and Watanabe (1952) identified eight polyploid seedlings of *Larix kaempferi* Sarg. among two-year-old nursery transplants. Of these six were apparently tetraploids, whereas the remaining two were mixoploids, that is, part diploid and part tetraploid. A triploid seedling was discovered in the progeny of a *Larix decidua* × *Larix occidentalis* Nutt. cross (Larsen and Westergaard, 1938), and the authors postulated that this triploid hybrid was the result of a union between a normal (haploid) egg cell of *Larix decidua* and a diploid (unreduced) pollen grain of *Larix occidentalis*.

The only report of a natural polyploid pine seedling was made by Zinnai (1952). He located five tetraploid *Pinus densiflora* Sieb and Zucc. seedlings in transplant beds.

The morphology of the polyploid individuals described in the aforementioned reports can be summarized as follows: The cells were larger than those of diploids, the needles were thicker and shorter (except for the triploid larch which had longer needles), the foliage was dark green, the guard cells were larger, the number of stomates per unit area was reduced, the growth was irregular and depressed, the size of the pollen grains was variable, and pollen viability was reduced. Whenever mixoploid seedlings were located, their root system was diploid with the shoot being polyploid. In no instance was a mixoploid located which had a polyploid root system and a diploid shoot.

Despite a great number of letters of inquiry written to forest geneticists and cytologists in the United States and abroad, no further reports of verified polyploid pine trees were located, although the occurrence of polyploid individuals was postulated by several of the correspondents.

Materials and Methods

The abnormal seedlings were collected in the Florida State Nursery at Olustee, Florida, where some 40 million slash pine seedlings are grown annually. The nursery beds were surveyed for abnormal seedlings at various times during seven growing seasons; the first collection being made during September of 1952 and the last during February, 1957. The greatest number of abnormal seedlings was located when they were about 3 months old. At this stage their needles had a bluish hue, and the neighboring normal seedlings had not yet had time to crowd out the slower growing abnormal types. At this age, the frequency of abnormal seedlings was about 0.0002 percent, and they occurred singly and at random throughout the beds. As the season progressed, the apparent percentage of abnormal seedlings decreased, presumably because they were unable to survive, or were crowded out by the larger, more vigorous seedlings. Over 50 abnormal seedlings were dug up and potted in fertile soil and moved to a greenhouse. The results reported here refer to five of these seedlings only, because the others did not survive, or because accurate chromosome counts could not be made from the survivors. All of the abnormal seedlings had under-developed root systems, and many lacked lateral roots. In those instances when lateral roots were present they were short and club-shaped.

To obtain vigorous growth for the chromosome counts, soluble fertilizer was added to the soil and the plants were kept under a 17-hour photoperiod for several weeks before material was collected for analysis. Normal seedlings (controls) were treated in the same manner.

To obtain chromosome configuration in the metaphase stage the treating schedule of Mergen and Novotny (1957) was followed. Actively growing buds, and root tips, 3-8 mm. long, were used. The vegetative needle buds supplied sufficient meristematic tissue with mitotic divisions to make chromosome counts possible. On the other hand, chromosome counts could be made from only a few squashes of root tips. The chromosomes were counted by drawing idiograms at an approximate enlargement of 2000X with the aid of a camera lucida, or a projection mirror.

Tangential and transverse sections were prepared from several of the terminal buds to determine the location of the polyploid or abnormal cells. The buds were fixed in Navashin solution before they were embedded in Tissuemat. Serial sections were cut at 10 to 12 μ, and were stained with crystal violet, iodine, and eosin.

To obtain representative samples from the needles, 5 mm. segments were cut at a distance from the base equal to 20 percent of the total length of the needle. This was necessary because the needles varied in length from 20 to 120 mm.

Cross-sections were made from the segments of fully-grown secondary needles, with the exception of those from seedling number 5, which had not developed secondary needles. In this instance primary needles were examined. The segments were fixed in FAA, dehydrated, embedded in Tissuemat, and cross-sections were cut at a thickness of 15 μ. The sections were stained by using a modification of the safranin-aniline blue method and mounted into permanent slides.

The arrangement of the stomates was determined on the outer face of the needles. The needle segments were macerated at room temperature for 1½ to 2 hours in a 1:1 mixture of 20 percent hydrochloric acid and 35 percent nitric acid. After this treatment the epidermis, along with some cells of the hypodermis, could be separated from the subjacent cell layers. The epidermis was briefly rinsed in water and stained for 10 seconds in a 0.5 percent alcoholic safranin solution. This was followed by dehydration in an alcohol series, clearing in xylene, and embedding in Permount. Rapid work was necessary because the epidermis sections tended to curl in the xylene.

The openings of the stomates were measured with an ocular micrometer (X430), and from each plant 10 stomates were measured on each of 5 needle segments. The same needle sections were also used for a count of the teeth along the edges.

Results

In view of the fact that the seedlings were highly variable, and since they represent the first polyploid pines to be described morphologically, it was thought best to treat each of the seedlings separately, rather than generalize on their appearance.

The average values on the anatomy of the needles from the five abnormal seedlings, along with the values for a normal diploid seedling are summarized in Table 1.

Normal diploid seedlings. The characteristic features of an average diploid slash pine seedling are illustrated in Figure 1. When the seedling was photographed it was 2 years old, and bore only secondary needles. The anatomy of the needles was similar to that described for slash pine by Sutherland (1954); the stomates appeared in straight rows and were uniform in appearance. The chromosome number of mitotic figures in somatic tissue was verified to be 24, as had been reported previously by Sax and Sax (1933), and by Mehra and Khoshoo (1956).

Abnormal seedling number 1. Seedling number 1 grew very slowly, being 20 cm. tall after three years (Fig. 2). The branches, to the extent that they were pres-

TABLE 1. *Characteristics of the needles in the abnormal seedlings and a control seedling.*

Seedling	Needle length (mm.)	Needle width (mm.)	Rows of stomates (total number)	Rows of stomates per mm. of needle width	Stomates per unit length	Teeth per unit length	Average Stomate D'a. (μ) Outer face of needle	Inner face of needle
Control (2n)	115	1.00	9.6	9.6	9.1	3.7	37.6	36.7
Abnormal seedlings:								
1	35	1.45	7.6	5.2	8.9	1.2	44.5	42.6
2	22	1.32	6.8	5.1	9.3	2.4	35.0	36.9
4	96	1.53	7.9	5.2	8.7	2.8	51.8	50.1
5	17	1.01	6.3	6.2	7.0	1.2	35.9	32.3
6	121	1.60	6.5	4.1	8.1	2.6	43.2	44.0

ent, had not elongated more than about 1 cm. Most of the needles were primary, but there were a few short and exceptionally thick secondary needles.

About 65 percent of the secondary needle buds dried and fell off before they were 5 mm. long. The needles, as well as the growing shoot, were dark green with a bluish hue. Their surfaces were rough with many ridges and expanded teeth. The thickness of the hypodermis was not uniform but was greater under the ridges, and the roughness of the outer surfaces was also reflected in the irregularity of the endodermis. There was a well-developed mesophyll but the number of resin ducts was lower than in the normal seedlings. The stomates appeared in uneven rows; both the spacing within the rows and between the rows was irregular, and, as indicated in Table 1, the stomates had a larger diameter than those in the normal seedlings.

Chromosome counts indicated that the majority of cells were tetraploid ($4n = 48$). Normal diploid cells were also present and these occurred in the needle bases in an approximate ratio of 1:4 tetraploid cells, whereas in the root tips the ratio of diploid to polyploid cells was about 1:2. No cells with triploid sets of chromosomes were found. As a result of the slow growth of the seedling only a few cells with dividing chromosomes were obtained. However, the number of clear nuclear plates was sufficient to establish with certainty that the seedling was made up of both diploid and tetraploid cells.

Abnormal seedling number 2. Seedling number 2 was slow-growing and after 3 years it had a height of 15.5 cm. (Fig. 3). The secondary needles appeared singly, and in some instances there was a partial split through the middle, indicating that two needles from one fascicle had fused together. In addition to being very short, the needles started to curve and had the appearance of claws. The root system was poorly developed, and consisted of an enlarged growing knob with several short laterals above it, and there were no mycorrhizae. The cross-sections through the needles showed a very distorted arrangement of the anatomy; the resin ducts were present in only one half of the needle, and the cells of the plicate mesophyll were arranged and oriented differently in the two halves. Teeth were present on the various ridges, and their arrangement did not appear to follow a definite pattern. The stomates occurred in irregular partial rows, and were slightly smaller than those in the normal seedlings.

The chromosome count showed that the seedling was a mixoploid and was made up of diploid, triploid and tetraploid cells, with the majority of cells having 48 chromo-

somes. The ratio of diploid cells to tetraploid cells was 1:4.5; the frequency of triploid cells was about 1:10. The chromosomes were longer than those in normal seedlings, and it was difficult to spread the chromosomes in one plane without rupturing the cell walls. No satisfactory chromosome plates were obtained from the root tips.

Abnormal seedling number 4.[1] While in the seedbed, seedling number 4 had dark bluish needles that were quite thick and long. The height growth was somewhat slower than that of the surrounding seedlings and the hypocotyl and the growing

[1]Abnormal seedling number 3 was not suitable for cytological analysis.

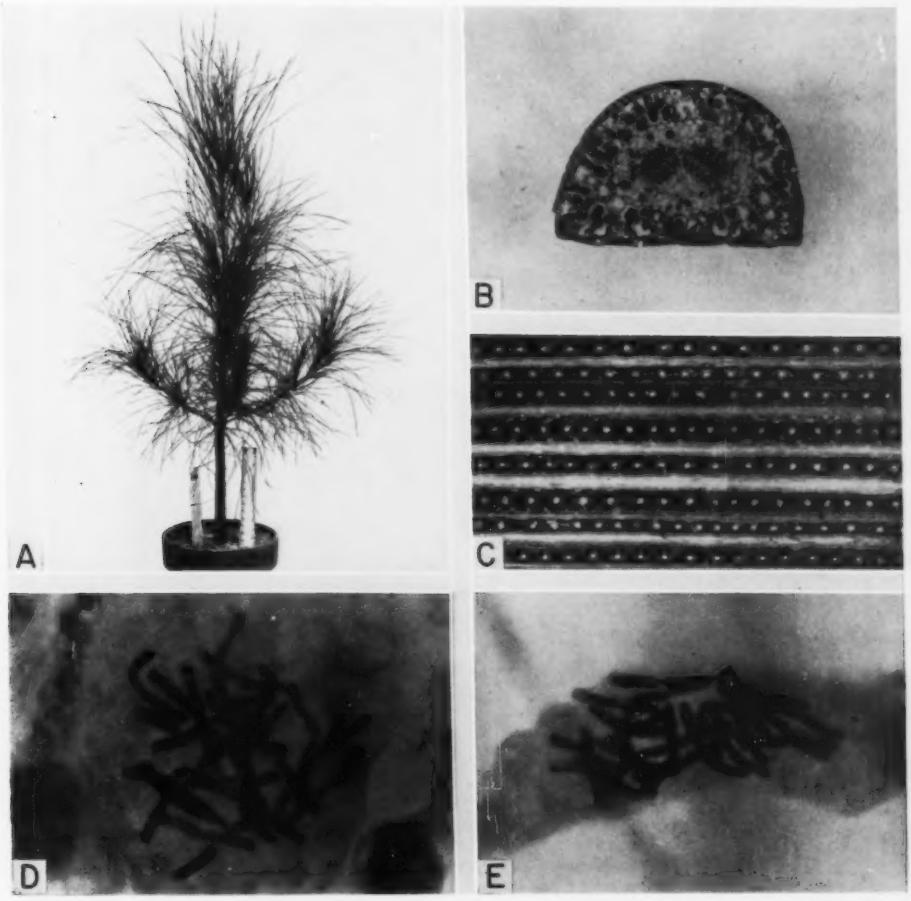

FIGURE 1. *Normal slash pine seedling. A. Seedling two years old. B. Cross-section through secondary needle, X30. C. Arrangement of the stomates on the outer face of a secondary needle, X30. D. + E. Chromosomes in metaphase, X1000 (2n = 24).*

points were thick and succulent. After the early seedling stage, its morphology did not differ appreciably from that of normal seedlings, with the exception of the secondary needles which were much thicker. The height growth also remained slower, and

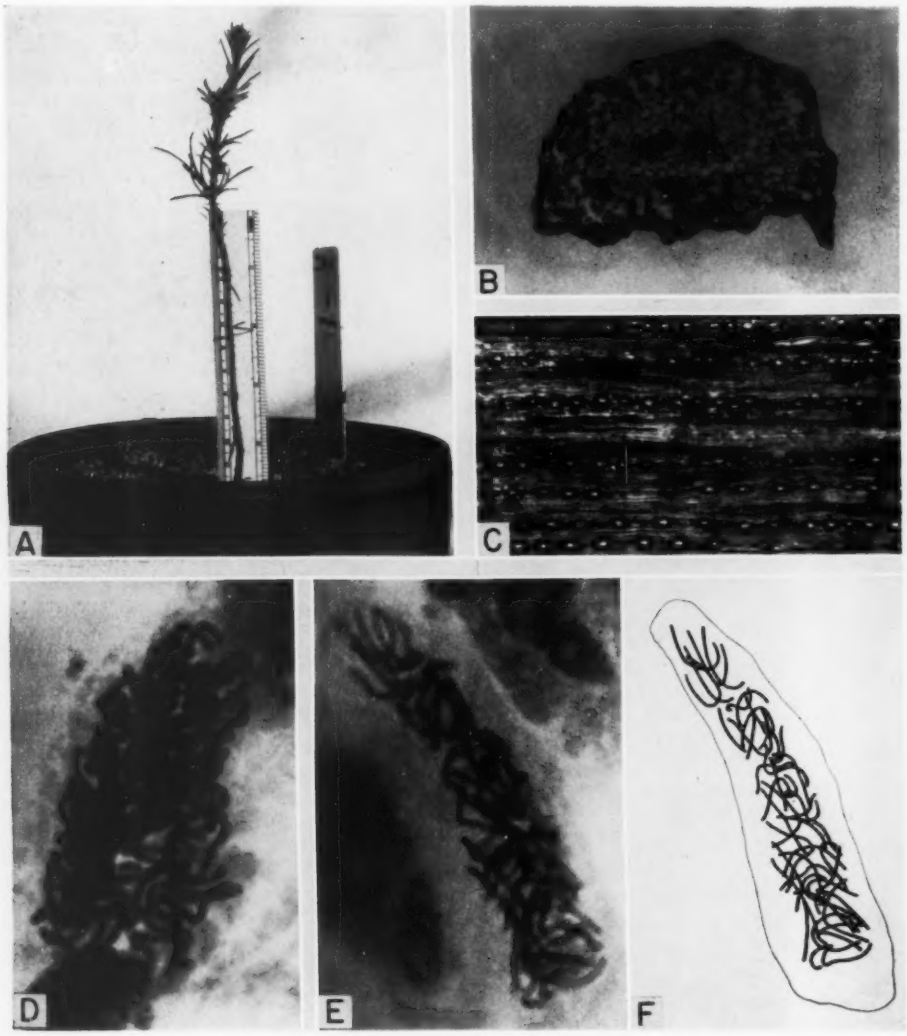

FIGURE 2. *Abnormal seedling number 1. A. Appearance of seedling at the age of three years. B. Cross-section of a secondary needle, X30. C. Arrangement of the stomates on the outer face of a secondary needle, X30. D. Polyploid cell in early anaphase, probably 96 chromosomes, X1100 (4n = 48). E. Tetraploid cell, X1100 (4n = 48). F. Idiogram of chromosome complement of cell in E traced with a camera lucida.*

after 3 years it had formed only one side branch which was 3 cm. long (Fig. 4). The root system consisted of one main root with several well-branched lateral roots, and the roots ended in enlarged knobs which were brittle. The needles were

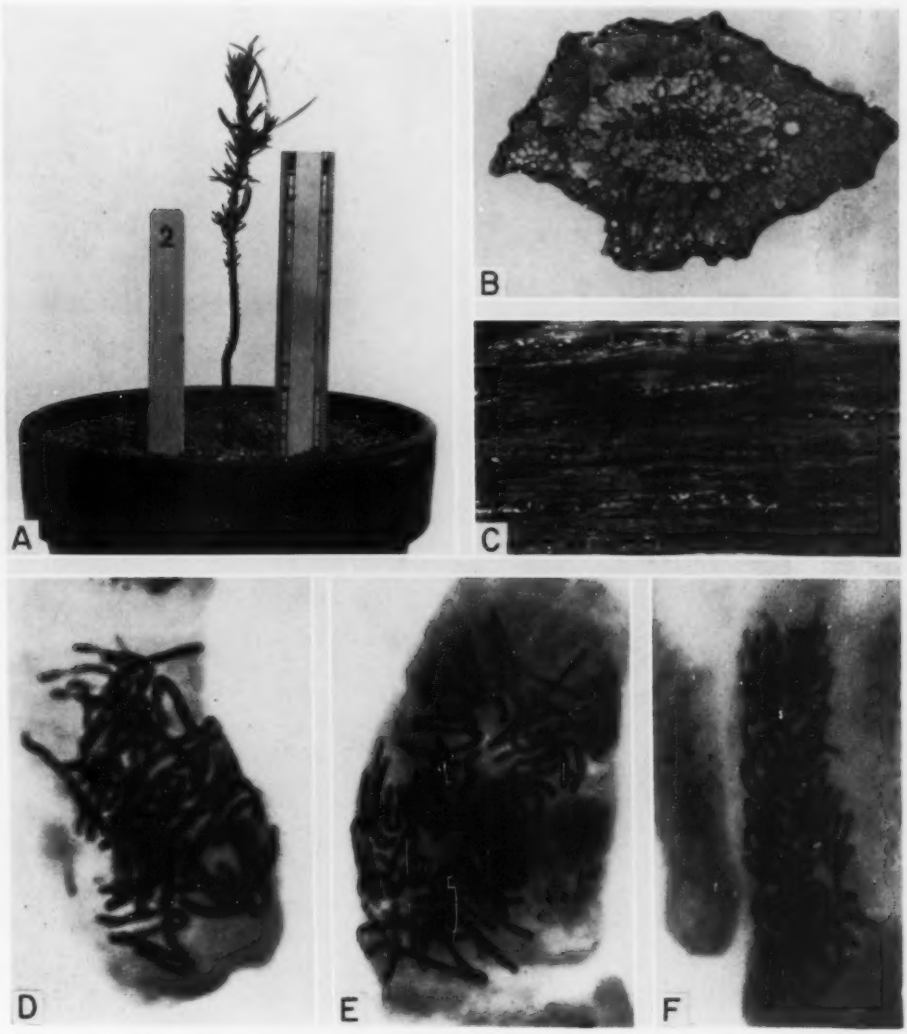

FIGURE 3. *Abnormal seedling number 2.* **A.** *Appearance of seedling at the age of three years.* *B. Cross-section through a secondary needle, X30. C. Irregular arrangement of stomates, X30. D. + E. Tetraploid cells, X1100 (4n = 48). F. Cell with ± 72 chromosomes. Probably an anaphase of a triploid cell, X1000 (3n = 36).*

1.60 mm. wide as compared to 0.99 mm. in the normal seedlings. The anatomy of the needle appeared normal, with the exception of the stomates which were arranged in uneven rows and were much larger, their diameter on the outer surface

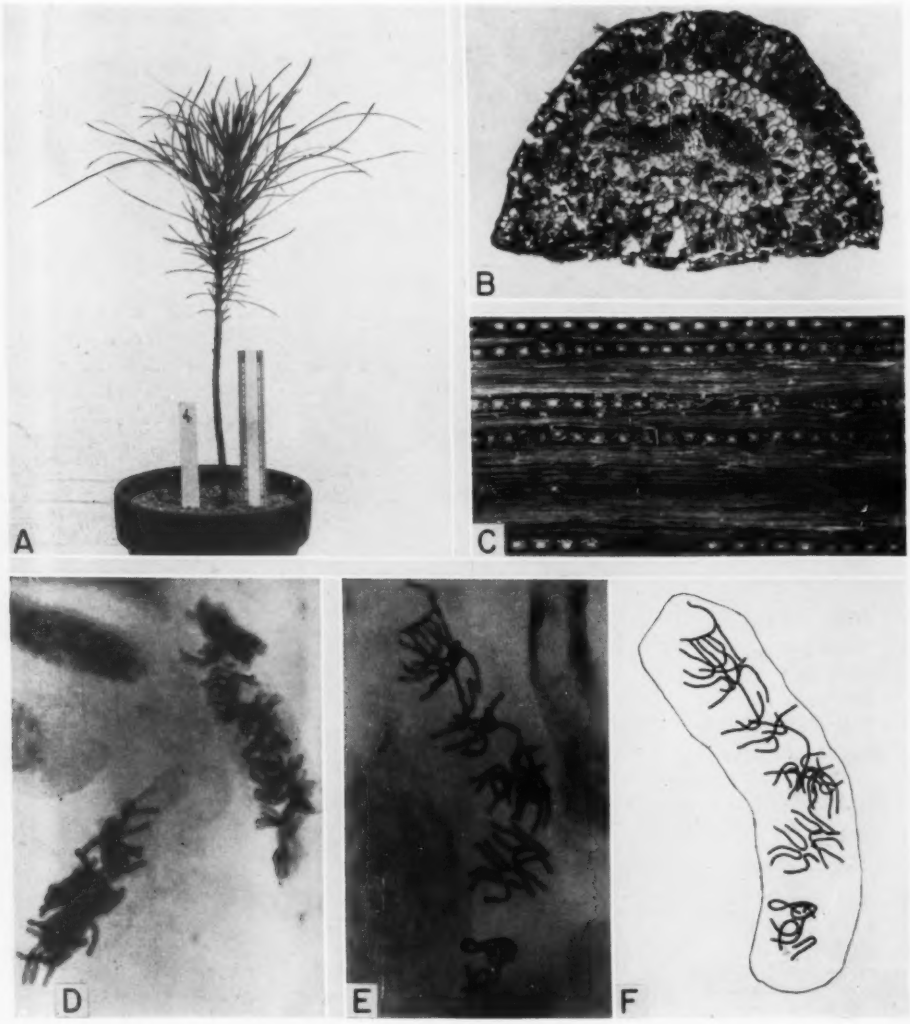

FIGURE 4. *Abnormal seedling number 4. A. Appearance of the seedling at the age of three years. B. Cross-section through secondary needle X30. C. Arrangement of the stomates, X30. Note the large size. D. Two triploid cells, X500 (3n = 36). Chromosomes in cell in upper right corner have just separated. E. Triploid cell, X800 (3n = 36). F. Idiogram of cell in E.*

being the largest (51.8μ) in any of the seedlings examined.

Chromosome counts showed seedling number 4 to be a mixoploid. It differed from the other plants by its relatively high frequency of polyploid cells in the bases of

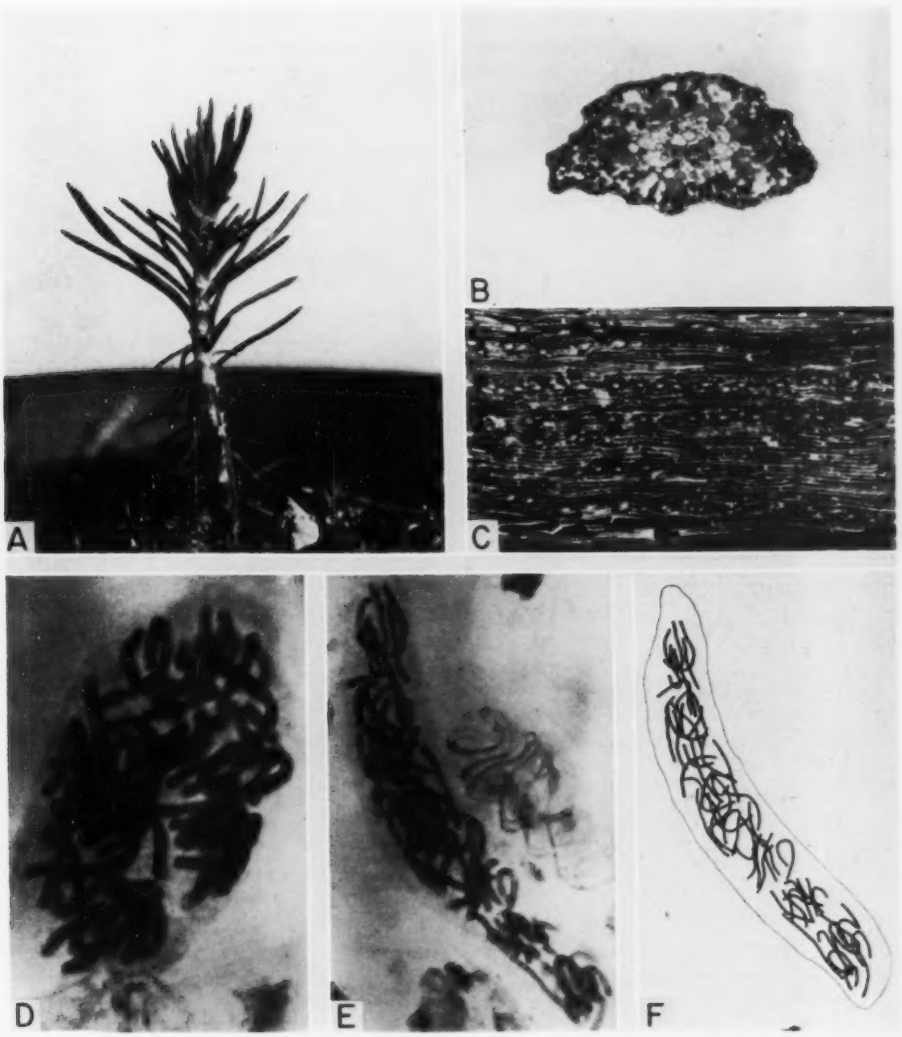

FIGURE 5. *Abnormal seedling number 5. A. Appearance of the seedling at the age of 18 months. X1.1. B. Cross-section through primary needle, X40. C. Irregular arrangement of stomates on outer face of needle, X30. D. Tetraploid cell in metaphase, X1200 ($4n=48$). E. Heteroploid cell with 54 chromosomes. X800. F. Idiogram of chromosome complement of cell in E.*

the needles—13 polyploid cells to one diploid cell. Of the polyploid cells, about ¾ were tetraploid and the remainder were triploid. The number of triploid cells was higher in the other trees studied, and the ratio of diploid to polyploid cells in the root tips was 1:2. Several stages of mitosis could be observed in the dividing cells. There appeared to be no tendency for the chromosomes to move toward the equatorial plate during metaphase, and during anaphase the daughter chromatids remained in an apparently random location within the cell. This partial mitosis doubled the number of chromosomes within the cell because no cell wall formed to separate the daughter chromosomes.

Abnormal seedling number 5. Seedling number 5 was 18 months old when the photograph in Figure 5 was taken. At that time it was 4 cm. tall, and when it was 30 months old it had not formed any secondary needles. Therefore, all the descriptions of the needles refer to primary needles. Periodically, the seedling developed a large, succulent terminal bud but it took considerable time for the bud to enlarge. The root system was almost non-existent, and the growing point died back from time to time. Due to the extremely stunted growth, few slides were obtained which showed mitotic division.

The needles had a well-differentiated epidermis, but the hypodermis and the sclerenchyma cells were almost lacking in most of the slides examined. As compared to primary needles of diploid plants, the palisade layer was better developed and occupied about 4/5 of the cross-sectional area; the stomates occurred in irregular rows and were small.

From the slides that were prepared it was possible to establish that the plant was heteroploid. Idiograms were drawn from several diploid and some tetraploid cells, but no triploid cells were located. There were, however, several aneuploid cells which had a chromosome count of 54. The ratio of diploid to heteroploid cells was approximately 1:7.

Abnormal seedling number 6. When seedling number 6 was two years old, it was 19 cm. tall and had one lateral shoot that was about 1 cm. long (Fig. 6). It had formed secondary needles that were of normal length, but they were much thicker than those of the control seedlings, and they were irregularly distributed. The root system was comparatively well developed, but all the root tips were swollen and were club-like in appearance. The needles had a tendency to twist, and their surfaces were uneven. The anatomy, as viewed in cross-section, appeared normal with the exception of the ridges on the surfaces which were reflected as distortions throughout the sections. The distribution of the stomates, from row to row and within rows, was uniform.

Chromosome counts showed that seedling number 6 was also a mixoploid, the meristematic tissue of the buds being composed of cells with diploid and tetraploid chromosome complements. The ratio of tetraploid cells to diploid cells was 6:1. The ratio of tetraploid cells to diploid cells in the root tips was 1:2. No triploid cells were found. The number of chromosomes in several of the cells could not be established with certainty, especially in those cells which were in the anaphase stage. Figures 6E and 6F illustrate two polyploid cells in the anaphase stage. Although the precise number of the chromosomes in these cells could not be established, it was estimated that there were about 96 chromosomes in each of these cells, indicating a tetraploid condition in the somatic cell before mitosis.

Location of the Polyploid Cells

It was difficult to determine the exact location of the polyploid cells because once cell division had ceased, it was not possible to estimate its chromosome number by size alone. However, in several of the serial sections there were several dividing nuclei and almost all of the polyploid cells were found along the periphery; in some instances they occurred for a limited distance inside. They extended toward the center of the growing tip in only a few of the sections.

Discussion

Abnormal slash pine seedlings in nature are not rare, yet there are no reports in the forestry literature. The frequency of 0.0002 percent that was observed in the Olustee, Florida, nursery was undoubtedly lower

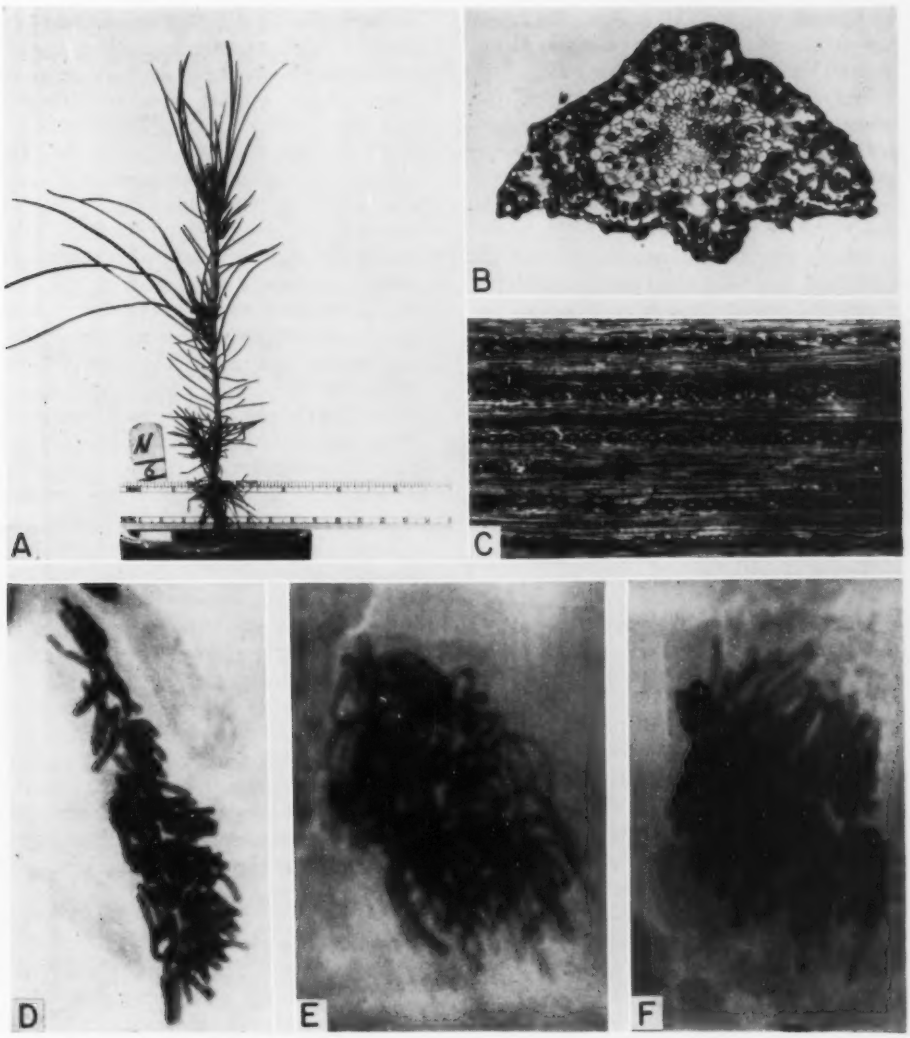

FIGURE 6. *Abnormal seedling number 6. A. Appearance of the seedling at the age of two years. B. Cross-section of a secondary needle, X30. C. Arrangement of stomates on the outer face of a secondary needle, X30. D. Tetraploid cell, X1000 (4n = 48). E. + F. Anaphase of polyploid cells, probably 96 chromosomes, X1300 (4n = 48).*

than that of the actual number which occurs in nature. These polyploid seedlings have a low capacity for survival because they lack the structures for adequate competition; the growth of both roots and shoots is depressed. The observed value of 0.0002 percent is somewhat lower than the frequency of polyploid seedlings that has been observed in the other members of the Pinaceae: 0.1 percent for *Pinus densiflora* (Zinnai, 1952), and 0.009 percent for *Picea abies* (Kiellander, 1950). Polyploid individuals are easiest located in the nursery beds where several million even-aged seedlings can be examined within a relatively short period of time. In addition, the selection is made from seedlings in a uniform and favorable environment, growing from seed which came from thousands of trees, scattered over millions of acres of forest land. In a natural forest it is much more difficult to isolate polyploid individuals because most of them have succumbed to the environment. Nevertheless, some abnormal slash pine trees have been located in and around the Olustee, Florida, area. Some of these have produced male and female flowers. The size of the pollen was measured from one of these "Mutant Pines," as they are called locally. When compared to normal slash pine pollen, the pollen from the "Mutant Pine" was smaller (49.5μ versus 52.5μ for the small diameter and 58.1μ versus 70.7μ for the large diameter). The germination count showed that almost all of the pollen grains from the abnormal slash pines were abortive and all of the seed obtained from these mutants was empty. No chromosome counts have been made on these larger trees.

In general appearance some of these mixoploids are very similar to slash pine trees that were treated with colchicine. Since none of the seedlings had polyploid cells throughout, these seedlings did not originate as the result of the fusion of unreduced (n) gametes or egg cells, but are the result of chromosome duplication after fertilization. They were not genetically uniform throughout the plant and therefore can be termed chimera (Chittenden, 1927). Cross-sections through some of the developing buds indicated the chimeras to be of the periclinal or mericlinal type. There were some indications that one of these mixoploid slash pine seedlings was the result of endomitotic divisions. In these endomitotic divisions there is a duplication of the chromosomes with a subsequent separation, but without the formation of a spindle or metaphase plate, and without cell division (Geither, 1941). Endopolyploid individuals have been described before in both the animal and plant kingdoms (Mickey, 1946; Berger, 1941; and Witkins, 1945). There was a certain degree of differentiation in the shape and size of the chromosomes between the different trees, but, due to the drastic chemical pretreatment during the maceration process, no attempt was made to evaluate these differences. Several cells were characterized by incomplete genomes but in these instances it was very difficult to verify the number present in the cells before maceration, as the long, thin chromosomes were crowded and tangled at the metaphase plate and in addition, the cell wall had ruptured in many instances allowing chromosomes to slip out and swim about in the mounting medium.

From a practical forestry standpoint these mixoploid seedlings have little value because of their low survival rate, and their low fertility. Perhaps some use might be made of some of these short-needled, slow-growing pines in ornamental work and in foundation plantings. These mixoploids are of little evolutionary value, because they are probably unable to form sexual tissues with balanced higher chromosome numbers.

Summary

Abnormal slash pine seedlings were collected in the Florida State Nursery and their morphology along with the results of a cytological study are reported. The frequency of these abnormal seedlings in the nursery beds was about 0.0002 percent, and their survival is greatly hindered because both their roots and shoots are de-

pressed. Five of these seedlings were verified to be mixoploids, having chromosome complements of 2n, 3n, and 4n. These mixoploid seedlings are probably of little evolutionary value, as they are unable to produce reproductive tissue with a balanced chromosome number.

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Role of Chemical Treatment in Stimulating Resin Flow

BY
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R. P. TRUE
C. S. SCHOPMEYER

THE MAJOR EXPENSE in producing resin by traditional methods is incurred in wounding trees at weekly intervals to renew the flow. Solodki and Vasskovskaya (1933) in Russia explored the possibilities of extending the period of flow in order to reduce labor costs. Theorizing that the flow stops because of crystallization of resin at the wound, or because of distention of epithelial cells into the lumen of the resin canal, they applied a large number of solvents, poisons, and electrolytes to fresh wounds on Scotch pine (*Pinus sylvestris* L.). Solvents were ineffective, but many strong electrolytes such as mineral acids brought about an increase in the rate and duration of resin flow. Sulfuric acid was selected as a cheap and effective reagent for further research. With the use of sulfuric acid, Nikolaev and Sinelobov (1936) found that resin yields were as good from cambium-depth wounds as from the customary wounds extending into the wood.

Hessenland (1935) and Kublun (1936) tested a large number of acids, bases, salts, and organic compounds on Scotch pine in Germany. The increase in resin yield was greatest with 50 percent sulfuric acid (128-percent increase) and 10 percent potassium hydroxide (111-percent increase). They found that treatment with a strong mineral acid permitted extension of the wounding interval from 1 week to 2 weeks with no loss in yield per tree per season.

Research on the chemical treatment of wounds on naval stores pines in this country was begun on a limited scale in 1936 in the U. S. Department of Agriculture by the Forest Service and the Naval Stores Research Division of the old Bureau of Agricultural and Industrial Chemistry. This work has been expanded considerably by the Forest Service. Liefeld (1940), Mirov,[1] and Snow (1948 and 1954) obtained data on resin yields from slash pine (*Pinus elliottii* Engelm.) and longleaf pine (*P. palustris* Mill.) in Florida using many variations in size of wound, wounding frequency, and acid concentration. They obtained increases in resin yield resulting from acid treatment ranging from about 25 to 60

[1]Mirov, N. T. Report on naval stores work in Florida, March-July 1942. Unpublished office report, Southeast. For. Exp. Sta.

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percent depending on the acid concentration used and the species. These increases, however, were maintained only for 3 seasons of weekly wounding on the same trees. When the wounding and treating interval was extended to 2 weeks, a normal yield of resin was obtained with a saving of about half of the labor required for wounding. In general, the resin yield responses to acid treatment were very similar to those obtained on Scotch pine in Europe. These data provide additional evidence that acid treatment of wounds causes both an increase in flow rate and a prolongation of the period of flow between successive wounds.

The German and Russian workers had different opinions on the way in which acid brought about these responses. Hessenland 1935) believed that the application of acids caused a chemical stimulation of the manufacture of resin. Nikolaev and Sinelobov (1936) thought that the opening up of the radial ducts by physical action of the chemical was responsible for the increased flow.

A number of exploratory studies concerning the effects of acid treatment of wounds were made to determine which of these two theories is applicable. The results are reported here. The applied aspects of chemical treatment of naval stores pines are discussed by Snow (1954) and Dyer (1955). The method now in use is to spray about 1 ml. of sulfuric acid solution (50 percent by weight) on the freshly made wound.

Speed of Exudation Response

Some indirect evidence on the mechanism of the action of sulfuric acid on resin flow was provided by observations of the time interval required for measurable increase in exudation after treatment of fresh wounds with sulfuric acid. For this purpose, circular punch wounds ¾ inch in diameter were used. These wounds were made with a cylindrical leather punch and extended only to the cambial region. The resin flowed from the wound over a small metal gutter into a vial of 30 ml. capacity (Fig. 1), where its volume was determined from its height in the vial. The punch-wound method is particularly useful for observation of the course of exudation, because several dozen wounds can be placed on one tree, and the flow from each of them can be observed at short intervals. Errors arising from the estimation of volume of resin from its height in the vials can be controlled within practical limits by selecting vials of similar capacity after calibration with water.

Results from a representative test of the speed of the response to treatment with acid are shown in Figure 2. Each line is an average for eight punch wounds. Only one test was made on loblolly pine (*Pinus taeda* L.). Table 1 shows that this species responded to acid treatment between 15 and 30 minutes after wounding, or about as soon as a measurable quantity of resin was exuded. In longleaf pine, the response

FIGURE 1. *Series of punch wounds on longleaf pine used in studies of resin flow.*

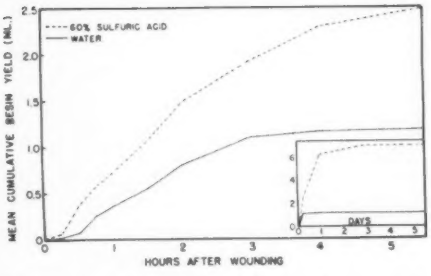

FIGURE 2. *Course of resin flow from punch wounds on loblolly pine. Eight fresh wounds were sprayed with water and eight with 60- percent sulfuric acid.*

was observed in about one-half hour in one test, but required several hours in another test. The resin of the latter species is more viscous and its flow from the ducts down to the vial is somewhat more delayed.

In a similar test on slash pine in which the fresh resin is still more viscous, acid-treated wounds yielded only 20 percent more resin in the first hour, and the difference was not statistically significant. However, the response usually occurs within the first day after treatment.

In general, the effect of acid on resin flow from freshly wounded tissue appears to be fairly rapid. At least part of the effect, therefore, appears to be a mechanical release of the resin already present in the ducts, the inference being that a systemic chemical stimulation of resin manufacture would require a longer period of time to be manifest in increased flow.

Localization of the Response to Acid

A second indirect line of evidence on the mechanism of the response to acid was provided by a study of the vertical distance over which the response occurred. Increased resin flow resulting from a physical effect of the acid should be quite localized. A chemical stimulation of the rate of resin synthesis might be either localized or more systemic in its effect.

The first test involved measurement of the flow of resin from punch wounds 1, 2, and 3 inches above two standard horizontal turpentine wounds on each of five large slash pines. The 10 standard wounds were first calibrated by measuring the resin yield from four successive weekly woundings, so that the standard wounds could be classed into two groups comparable in resin-yielding capacity. Then, at the time punch wounds were made, the standard wounds were renewed for the fifth time and half of them (one on each tree) were sprayed

TABLE 1. Mean cumulative yields of resin from acid-treated and water-treated punch wounds on one loblolly pine.

Time after wounding (hours)	Mean cumulative yields[1]		Standard error of difference	t[2]
	Acid treatment	Water treatment		
	Ml.	*Ml.*		
0.25	0.05	0.01	0.316	1.4
0.50	0.37	0.07	0.619	4.8
1.00	0.72	0.37	0.951	3.8
5.50	2.48	1.19	2.64	4.9

[1]Individual measurements made to nearest 0.05 ml.

[2]For 14 degrees of freedom, values above 3.0 are significant at the 1-percent level. The difference at 0.25 hour is not significant.

TABLE 2. Effect of sulfuric acid on mean yields from standard turpentine wounds and from punch wounds above them on five trees.

Treament of standard wounds	Mean yield of standard wounds in 1 week	Mean yield of untreated punch wounds at specified distances above standard streaks			
		1 inch	2 inches	3 inches	Total
	Ml.	*Ml.*	*Ml.*	*Ml.*	*Ml.*
Untreated	66.2	2.26	1.16	2.06	5.48
Sprayed with 40-percent H_2SO_4	127.8	1.02	1.22	0.70	2.94

with a solution of 40 percent sulfuric acid. Yields of resin measured June 30, 1944 (1 week after wounding and treating) are shown in Table 2.

In this test there was a clear superiority in resin flow from the standard streaks on which the acid was sprayed, but yields from punch wounds above acid-treated streaks were obviously no greater than yields above untreated streaks. Acid sprayed directly on one punch wound on one of the five trees resulted in a yield of 30 ml. of resin, in comparison with a mean flow of 1 ml. from the punch wounds 1 to 3 inches away from acid-treated streaks. Acid treatment of the standard wounds, therefore, did not stimulate resin flow from the untreated punch wounds above them.

A similar test on two longleaf trees involved 12 rows of 5 punch wounds each, spaced 2½ inches apart within rows (Fig. 3). The wounds extended ⅛ inch into the wood on one tree and only to the cambium on the second tree. Four of the twelve rows had no wounds treated with acid, and served only to show the normal flow from holes in each position in the row. In eight rows, the center wound was sprayed with 60 percent H_2SO_4 just after wounding on September 29. Yields of resin were measured 3 weeks later. Yields for the two depths of wounding showed the same trends and were combined.

Mean yields for the wounds in the various positions are as follows:

Lowermost untreated wounds	1.5 ml.
All other untreated wounds	0.4 ml.
Acid-treated center wounds	7.3 ml.

These data clearly show that stimulation of flow was practically, if not entirely, restricted to the wound on which the acid was applied.

FIGURE 3. *Rows of punch wounds 2½ inches apart within the row on longleaf pine. Center wound treated with sulfuric acid in 8 out of 12 rows.*

Acid-treated punch wounds ¾ inch in diameter have yielded as much as 60 ml. of resin in a week, in comparison with a mean of about 5 ml. from untreated wounds. This fact suggests that the extra flow from acid-treated wounds may be drawn from a considerable distance within the tree. It is unlikely that this much resin could be manufactured through local stimulation within an inch or so of the wound in a period of a few days.

Effect of Acid Applied to the Phloem

A third line of evidence was afforded by application of acid to the outer surface of the living phloem of longleaf pine exposed by removal of only the dead outer bark. Untreated patches of exposed phloem yield very little resin, probably because the radial resin ducts are usually occluded or very nearly occluded by parenchyma cells at the cambium and just inside the phellogen (Fig. 4, A, B, and C). However, when patches of phloem on longleaf pine are sprayed with 60 percent H_2SO_4, a resin blister forms at the cambium within several hours, and resin is soon exuded in much greater than normal quantities. The applied acid evidently allows escape of resin by collapsing the parenchyma cells which occlude or line the radial resin ducts. Anatomical observations on this point are discussed later.

The resin which accumulates in blisters under acid-treated phloem often develops sufficient pressure to rupture the phloem after several days. Very small, closed-end manometers made from fine glass tubes with mercury riders were inserted into a number of resin blisters, the outer surfaces of which had become more or less sealed by hardened resin. The mean of 30 maxima for short runs of less than 1 day, or of daily maxima for longer runs of the manometers was 0.22 atmospheres. The range was 0.12 to 0.40 atmospheres. The pressures recorded represent only those which the phloem blisters are capable of retaining, because resin exuded slowly from the surface of the blisters, and many of the blisters split open. Pressure in the resin duct system of the xylem is much greater. In later work, not yet published, resin exudation pressures ranging from 8 to 12 atm. were obtained on intact trees.

The fact that the resin is under pressure in the tree indicates that it should exude more rapidly, or that the flow rate should decrease more slowly, after treatments which enlarge any restriction in the openings of the ducts, particularly where these are normally closed, as in the radial ducts at the phellogen and at the cambium.

Anatomical Effects of Sulfuric Acid

Destructive action. The major rapid effect of 40- to 60-percent solutions of sulfuric acid applied to cambium-depth wounds is to cause collapse and partial disintegration of the parenchyma cells which occlude or surround the outer ends of radial resin ducts (Fig. 4, D and 4, F).

When a 50-percent solution of acid is used, this effect gradually extends from the upper edge of the wound to a height of about ¾ inch in the phloem and outer xylem over a period of about 1 week following treatment. Resin ducts opened in this manner continue to flow during the second week after treatment.

Another effect of sulfuric acid is to bring about minute concentrations of resin at the cambium region to a height of about ¾ inch above the wound (Fig. 4, E). A separation of the bark and wood follows, and is probably augmented by the shrinkage of phloem tissues toward the outer bark.

Induced structural changes. Munch (1919) suggested that resin flow from a wound is normally stopped by the ballooning of epithelial cells to form tylosoids in the resin ducts and that plasmolytic agents may prevent such action. We have not observed any ballooning of the cells lining the ducts near untreated wounds. However, it does appear that after the openings of ducts have been enlarged by the action of acid, they would be less readily occluded

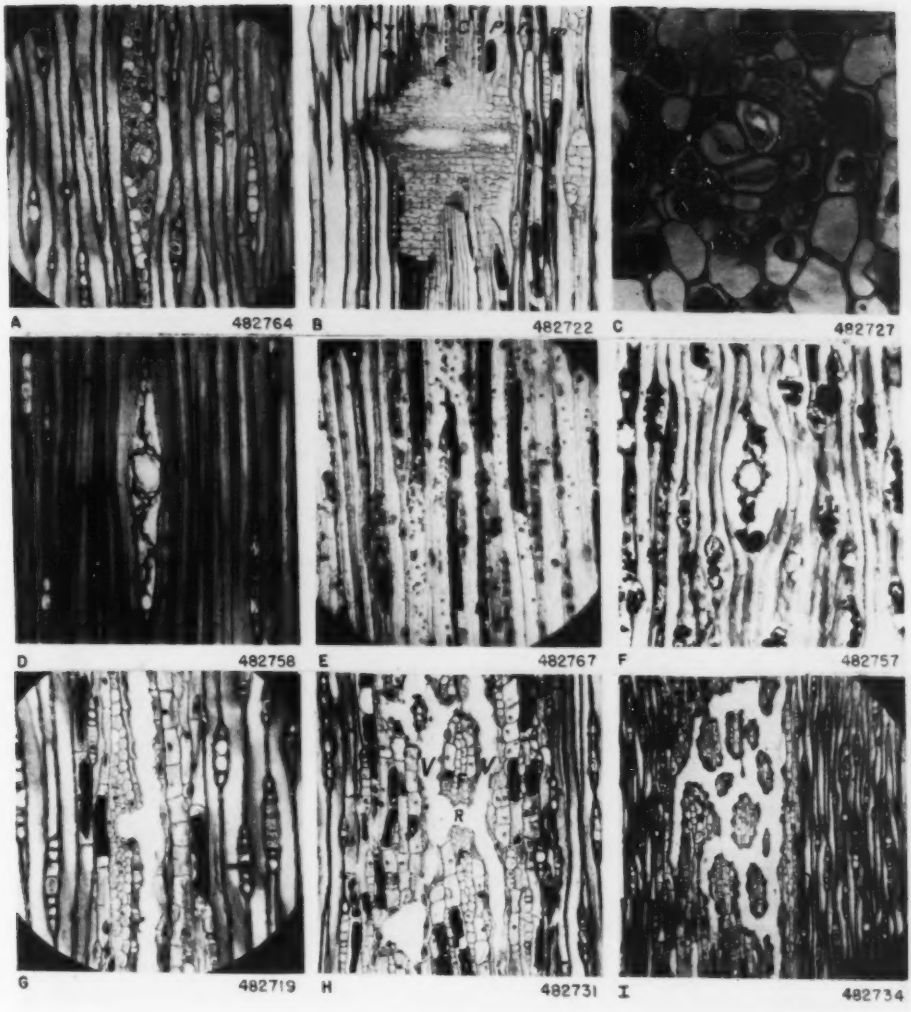

FIGURE 4. *A. Radial resin duct in tangential section of xylem near cambium showing closure by four large epithelial cells. B. An almost radial section through a fusiform ray showing closure of radial resin duct at cambium. C. Radial resin duct in tangential section of phloem near phellogen showing closure by three large epithelial cells. D. Radial resin duct in xylem near cambium after treatment with sulfuric acid showing wide opening resulting from collapse of epithelial cells and the surrounding parenchymatous cells of the fusiform ray. E. Tangential section through cambium above wound after treatment of wound with sulfuric acid. Cells contain small globules of resin. F. Same as D but in phloem. Tangential sections G, H, and I are all from xylem about 5 cm. above acid-treated wounds. G. Junction of a radial and a longitudinal resin duct. H. Fusiform ray F contains a radial duct R connected with two vertical ducts V, both of which are enclosed in a vertical strand of parenchyma. I. Tangential section in xylem above the zone of acid injury through a broad band of proliferated vertical parenchyma enclosing anastomotic resin ducts.*

by the hardening of oleoresin at the outlet.

Gore and Traubenhaus (1931) found that acid injury to roots of cotton increased the meristematic activity in parenchyma. We have observed similar effects in the xylem of longleaf pine. Acid-treated wounds apparently stimulated the cambium above the acid-killed zone to produce the large proportion of parenchyma and the anastomosis of resin ducts within this parenchyma shown in Figure 4, I. Figures 4, G, H, and I, however, were all made from sections taken in June about 2 inches above the last of a series of eight acid-treated wounds made at weekly intervals on a single longleaf pine. Figure 4, H shows a lesser degree of proliferation than 4, I. Figure 4, G shows a single vertical resin duct at a junction with a radial duct, but no proliferation of surrounding parenchyma is apparent. The number of such single vertical resin ducts, however, may also be increased as a result of an acid-treated wound stimulus.

After untreated wounds ¼ inch high were cut into the wood at weekly intervals for 4 months, Gerry (1931) observed a tenfold increase in number of vertical resin ducts per unit area of transverse section through the current growth ring directly above the last wound as compared to the average for the 3 years preceding the wounding. It is obvious, therefore, that the increase in number of resin ducts is a result of a traumatic stimulus which may be caused by either untreated wounds cut into the xylem or by acid-treated, cambium-depth wounds. No data are available on whether this traumatic stimulus is greater in acid-treated wounds than in untreated wounds.

Such ducts cannot contribute to the increased flow rate obtained by acid treatment of an initial wound on a tree, because the response is obtained before traumatic ducts are formed.

Gerry (1931) states that many of the traumatic resin ducts are very short and are formed throughout the current growth ring. She found that fewer of these traumatic ducts were present at the end of a season of wounding where wounds were cut ½ inch high than where they were cut ¼ inch high.

With cambium-depth, acid-treated wounds, all traumatic ducts remain in place and presumably contribute to the resin content of the tree through connections with either normal longitudinal or radial resin ducts.

With acid-treated wounds cut into the wood, traumatic ducts are also formed for a short distance above each successive wound as in Figure 4, H and 4, I. Such ducts, however, are cut out a few weeks after they are formed when subsequent wounds are made. Hence, fewer traumatic ducts are present at any time where wounds are cut into the wood than where they are cut only to the cambium. In spite of this difference in number of traumatic ducts, Snow (1948 and 1954) obtained equal resin yields with the two types of wounding using the same acid treatment on each. Therefore, the number of traumatic ducts present is probably not a contributing factor to the increase in resin yields obtained with acid treatment.

Plasmolytic Activity of Effective Chemicals

Snow (1944) listed several strong plasmolytic agents among the inorganic acids, bases, and salts which caused an increase in the exudation rate of resin from slash and longleaf pine. Sulfuric acid is the cheapest and most effective of the common inorganic chemicals in these classes. One measure of the effectiveness of a chemical as a plasmolytic agent is the freezing point depression per mol of solute at the eutectic mixture. This measurement is an approximate index of the effectiveness of inorganic chemicals in increasing the exudation rate of resin after a single application.

Ferric chloride, which has a higher freezing-point depression per mol than sulfuric acid, caused a higher yield of resin on

an initial wound. Yields on subsequent wounds, however, declined sharply because the height of killed tissue above the wound exceeded the height of tissue normally removed at each rewounding. To be effective, the chemical must be applied to live tissue exposed by wounding. Therefore, ferric chloride is not satisfactory for commercial use.

The killed tissue resulting from the upward diffusion of sulfuric acid from the sprayed wound is rather sharply limited to a zone ranging in height from 0.5 to 0.75 inch. Apparently this limitation is brought about by the buffering action of the cell sap of the tissues involved. This very desirable limitation does not occur when strong solutions of inorganic salts are used.

Effect of Acid With Frequent Wounding

Another approach to determining the nature of the effect of acid treatment on resin yields made use of a very high wounding frequency. The time interval between wounds was only 12 hours. With this frequency of wounding, rapid draining of resin will occur, and the rate of flow of resin out of the duct system can be expected to exceed the rate at which resin is put into the duct system by the biochemical reactions in the tree. Under this condition, if acid treatment of wounds causes an increase in the rate at which resin is synthesized in the tree, such an increase should be reflected in a higher rate of flow from the duct system than that obtained without acid treatment of wounds.

To test this hypothesis, two balanced groups of 10 trees each were wounded at 8:00 a.m. and 8:00 p.m. every day during a period of 14 days beginning July 26, 1949. A standard wound size, 6 inches wide, ½ inch high, and ½ inch into the wood radially, was used on all trees. Resin yields were weighed to the nearest gram for each tree immediately before each wound was made. In one group of trees all wounds were sprayed with a 50-percent solution of sulfuric acid. In the second group, wounds were left untreated. In later experiments, the lateral penetration of acid was found to be about ½ inch on each side of the wound surface. Such penetration increases the nominal wound width, which in turn results in greater yields. Therefore, the observed yields from the acid-treated wounds in this test were reduced by 1/7 to correct them for the extra inch of face width obtained from the lateral penetration of acid. Table 3 lists only the corrected values.

The previously noted rapid response to sulfuric acid was apparent on the first day, when yields from the acid-treated wounds were 50 percent greater than from the untreated wounds (Table 3). This increase was soon nullified, however, by lower yields from the acid-treated wounds made on the third and fourth days.

TABLE 3. Total daily resin yields on 10 trees wounded every 12 hours during a period of 14 days.

Day	Wound treatment	
	Acid	Untreated
	Grams	*Grams*
1	731	485
2	492	450
3	388	591
4	496	630
5	687	663
6	636	650
7	557	572
8	591	405
9	483	391
10	403	368
11	552	631
12	555	575
13	416	446
14	323	498
Total resin in cups	7,310	7,355
Scraped from face	507	306
Total yield	7,817	7,661

Apparently the acid caused a quick release of the resin stored in the tree at the time of the first wound. During the first 2 days, most of the yield probably consisted of this stored resin. On the third day, flow was at a minimum and may represent the end of draining of stored resin. The subsequent increase in daily flow on the fourth and fifth days may represent a delayed response in the resin-forming processes in the tree in adjusting to the disturbance in the pressure equilibrium of the resin duct system caused by the initial draining.

Flow from the untreated wounds made during the first 2 days apparently was restricted, and the pressure equilibrium was not displaced as far as in the acid-treated group. The time lag between the initiation of draining and the response in the resin-forming reactions, however, was apparently the same as in the acid-treated group because both groups reached a peak flow on the fifth day.

Total yields from the two groups of trees (Table 3) were not significantly different at the 5-percent level. Therefore, the acid treatment did not appreciably increase the yield of resin per unit width of wound over that obtained by mechanical wounding alone during the period of this test.

The next step was to determine whether daily yields in this test were a measure of the daily rate of production within the segment of the tree which was tapped. If the number of open resin ducts is not a limiting factor, the resin produced in the tapped segment of the tree will drain out as fast as it is produced.

The number of open resin ducts was not a limiting factor, as demonstrated by data obtained during the last 3 days of the test. During this period resin was collected separately from two portions of the aggregate wound surface. Two cups were installed on each tree. The cup that had been installed at the base of the tree when the experiment started was left in place. A second cup was installed on each tree near the upper edge of the wound surface so as to collect only the resin from wounds made during the last 3 days.

The yields (Table 4) show that the acid-treated wounds made during the first 11 days of the test were still contributing 43 percent of the total yield obtained during the last 3 days, while the new wounds above them produced 57 percent. On the untreated trees, only 12 percent of the total yield for the last 3 days came from the older lower wounds, and 88 percent came from the new wounds above.

These results indicate that a greater number of resin ducts remained open for resin flow during the last 3 days of the test on the acid-treated wound surface than on the untreated wound surface. Since the total yield from the trees with acid-treated wounds during the last 3 days was slightly less than that from the trees with untreated wounds, flow of resin must have been limited only by the ability of the trees to pro-

TABLE 4. Yields during the last 3 days of test showing portion obtained from previous wounds made during first 11 days (lower cup) and portion from current wounds made during this 3-day period (upper cup).

Wound treatment	Lower cup (old streaks)		Upper cup (new streaks)		Total for both cups
	Grams	*% of total*	*Grams*	*% of total*	*Grams*
Acid	555	43	738	57	1,294
Untreated	176	12	1,343	88	1,519

duce and not by the number of open resin ducts.

In this test two points of fact were established. Flow was unrestricted in both treatments, at least during the last 10 days, and yields were not significantly different for the two treatments. The conclusion is that acid treatment of wounds did not stimulate the resin-forming processes in these trees to a greater extent than mechanical wounding alone.

Conclusion

Although increased yields of resin can be obtained by spraying wounds with strong solutions of sulfuric acid (40 to 60 percent), the empirical facts described here indicate strongly that this acid does not stimulate the production of resin in the tree, but merely facilitates the outflow by prolonging the time during which resin ducts remain open after wounding. The pressure equilibrium in the resin duct system may be displaced sufficiently by the more rapid draining associated with acid treatment to result indirectly in a higher rate of resin production than is obtained with mechanical wounding. Where this occurs, the frequency of mechanical wounding is obviously not great enough to utilize fully the capacity of the tree to produce resin.

Summary

Solutions of sulfuric acid (40 to 60 percent by weight) and other strong electrolytes have been used successfully to increase the rate and duration of resin flow from fresh wounds on naval stores pines.

The following evidence on the mechanism of response was derived from studies of the chemical treatment of turpentine wounds on slash, longleaf, and loblolly pines:

1. In loblolly pine, which has resin of low viscosity, sulfuric acid treatment of a fresh wound resulted in an increase in the initial rate of exudation of resin. The rate of increase is slower and more variable in longleaf and slash pines, which have more viscous resin.

2. The increase in resin flow from a wound treated with acid did not extend to an untreated wound 1 to 3 inches higher up the tree.

3. Treatment of phloem in situ with acid causes resin to collect under pressure in a blister at the cambium, and to exude through the phloem.

4. Sulfuric acid causes destruction of the cambium for about ¾ inch above a wound and taps radial ducts in this zone where they adjoin the cambium.

5. Sulfuric acid enlarges the openings of radial resin ducts near the cambium by collapsing or destroying the epithelial and ray parenchyma.

6. Formation of short multiple resin ducts in wide bands of vertical parenchyma has been observed 2 inches above acid-treated wounds and above untreated wounds cut into the wood. These traumatic ducts probably do not account for the increase in resin yields obtained with acid treatment.

7. Resin was drained faster than it was synthesized in the tree by successive wounds made every 12 hours during a period of 14 days. At this frequency, yields from acid-treated wounds were not significantly greater than from untreated wounds. Hence acid did not cause an increase in the apparent rate of synthesis of resin.

8. The available evidence suggests that sulfuric acid treatment serves chiefly to facilitate the outflow of resin from the duct system.

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Ninth International Botanical Congress to be in Canada in 1959

MONTREAL, QUEBEC, CANADA, is the locale of this international meeting of plant scientists to be held at McGill University and the University of Montreal from August 19 to 29, 1959. The program as tentatively organized includes 16 sections, among them forest botany, nomenclature (August 16 to 19), taxonomy and geographiy of vascular plants, phytopathology, morphology and anatomy, physiology, ecology, and cytology and genetics. Field trips to various parts of Canada are planned both before and after the congress. Some are general and others for special purposes, for example, forest botany in Ontario and in Quebec.

Membership in the Ninth International Botanical Congress will be open to all persons interested in botany. The first circular with preliminary information and queestionnaire was issued January 31. The second circular will be sent only to those who returned the questionnaire or who ask to be placed on the mailing list. Those wishing to be placed on the mailing list or desiring further information may write to the Secretary-General, IX International Botanical Congress, Sicence Service Building, Ottawa, Canada.

International botanical congresses are held at intervals of about five years. All previous ones except that at Cornell University in 1926 were in Europe.

Effects of Fertilization and Thinning On Chemical Composition, Growth, and Specific Gravity of Young Douglas-Fir

BY
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GREGORY M. G. LAMBERT

FERTILIZATION of forest stands is likely to be tried more and more in forest management in efforts to improve growth on the poorer sites. In evaluating the results of such treatments it is necessary to know if they cause important changes in the chemical composition and the physical properties of wood. To assist in solving this problem an experiment was designed for studying the wood grown before and after fertilization and thinning on trees of a 30-year-old stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

In recent years an increasing number of studies have been made on the response of forest trees to fertilization—especially to application of nitrogen. A comprehensive bibliography with abstracts of this topic has been compiled by White and Leaf (1957). The response of young Douglas-fir to fertilization was studied for trees 10-15 years old (Gessel *et al.*, 1951; Gessel and Walker, 1956) and for 30-year-old trees (Shareeff, 1955; Gessel and Shareeff, 1957). The latter stand was fertilized to increase wood increment on trees approaching merchantable size; it was also thinned.

Wilde *et al.* (1951) have studied the relationship between different types of soils and the yield and quality of jack pine (*Pinus banksiana* Lamb.) pulpwood. Site conditions and the height in the tree at which the sample was taken influenced specific gravity of the wood and the alpha-cellulose content. However, when their data on the alpha-cellulose percent are plotted against either site index or rings per inch the correlation seems rather poor. The amount of alcohol-benzene solubles were slightly greater in the lower level of the stem than at the 25-foot height.

The rate of growth and composition of wood of quaking aspen (*Populus tremuloides* Michx.) and largetooth aspen (*Populus grandidentata* Michx.) in relation to natural soil fertility have been studied by Wilde and Paul (1948, 1951). They reported the lowest specific gravity and the lowest alpha-cellulose content from the areas having infertile soils. However, an examination of their data shows that the differences in specific gravity were small and the relationship did not hold in all instances.

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Materials and Methods

The trees used in the study described here were cut from four 1/10-acre sub-plots that had been established for the purpose of studying growth response to fertilization and thinning (Shareeff, 1955; Gessel and Shareeff, 1957). Since details of the area, soil, climate and the treatments are stated in their reports only a very brief description of the plots will be given here.

The four sub-plots were part of a single-acre plot in a stand growing on a gravelly outwash soil at the Charles Lathrop Pack Demonstration Forest, LaGrande, Washington. The area had been burned prior to the establishment of the present stand. The soil is gravelly sandy loam to a depth of 18 in. and gravelly loamy sand to a depth of 10-15 ft. The site index is 92, which is a high Site V for Douglas-fir.

The stocking in the plots used in this experiment was 3,700 trees per acre. Four 1/10-acre plots were assigned to the following treatments: control, thinning only, thinning and fertilization, and fertilization only. The thinning was based on the principle of crown thinning. The number of trees on each tenth-acre plot was: 355 on Plot 1N (unthinned and fertilized), 107 on Plot 2N (thinned and fertilized), 381 on Plot 1S (unthinned and unfertilized), and 92 trees on Plot 2S (thinned and unfertilized).

Fertilizer was applied in April, 1950, and in April of each succeeding year. Initial nitrogen application was at the rate of 100 lbs. of N per acre in the form of ammonium nitrate and ammonium phosphate. Also applied on a per-acre basis were P_2O_5, 150 lbs.; K_2O, 30 lbs.; and lime, 50 lbs. In the second year 100 lbs. of N in the form of urea were added, and in each of the next two years, 50 lbs. of N were applied. A total of 300 lbs. N per acre had been applied during a 4-year period.

In the fall of 1953, four growing seasons after the beginning of the experiment, four codominant trees were selected from each 1/10-acre plot. Average codominants in the thinned plots were selected by considering the relation of the tree to the neighboring stumps that represented the trees cut in the thinning operation and by observing the characteristics of the crown of the tree.

To avoid possible effects of proximity to either crown or base a 2-foot length of trunk was cut from each tree between 4 and 6 ft. above the ground. Discs from ½- to ¾-in. thick were cut and allowed to season to prevent growth of organisms, and to minimize chemical changes due to activity of parenchyma tissue. For specific gravity, percent summerwood, and growth measurement, discs were selected that were free from knots or defects. Four samples, one from each quadrant of the disc were cut from each of the two 4-year growth periods (1946-49 and 1950-53) representing the wood formed before and after the time of treatment. The wood of each 4 years was split out as small blocks or chips with a knife curved to the contour of the rings. The amount of summerwood and the total growth were measured on smooth-cut surfaces with the aid of magnifying lenses and a finely calibrated rule. Specific gravity for both growth periods was determined by the immersion method. The specific gravity reported for each growth period of 4 years was the average of 4 trees using 4 blocks per tree, one from each quadrant of that particular growth period. Specific gravity was expressed on the basis of oven-dry weight and volume when green (resoaked wood). All the wood used in this experiment was sapwood.

The analyses for ash, extractives, lignin, holocellulose, and alpha-cellulose were based on the procedures currently described in TAPPI Standards (1953). The wood of each 4-year period—before and after treatment—was separated from two or more discs by splitting. The wood chips produced were further re-split to match-size diameter and fed into a small Wiley mill. The knife settings and the screen used produced particles that passed through a 40-mesh screen with a minimum of fines

passing through an 80-mesh screen. Except in the holocellulose and alpha-cellulose tests, the analyses were made on the total wood samples that passed the 40-mesh screen. The solubles were determined successively on the same sample in the order: ether, alcohol-benzene, and hot water. These modifications of procedure are the same as those of Kurth (1948). For the celluloses, the particles used were those that passed a 40-mesh sieve but were retained on a 60-mesh sieve. Preliminary experiments showed that seven or eight chlorinations were optimum for preparing holocellulose. More than this caused a definite degradation with little or no change in whiteness and only a slight decrease in residual lignin. A preliminary test showed that residual lignin was present (0.3 percent) in the holocellulose even after 10 cycles of chlorination. Tests for residual lignin were run during the regular experiment on outer and inner samples of one tree on Plot 1N and on composite outer samples and composite inner samples from all the trees from Plot 1N. The tests on the individual tree gave 0.4 percent residual lignin in the holocellulose and the tests of the composite samples gave 0.5 percent residual lignin after 7 chlorinations. Therefore, it can be assumed that for these trees the amount of residual lignin in the holocellulose samples was approximately one-half percent. Lignin residue is a problem inherent to empirical methods of cellulose analysis. It was impracticable to make extra holocellulose determinations on all the wood samples for purposes of checking the lignin content. It was believed that the purposes of the experiment would be better served by using the holocellulose for determining alpha-cellulose content.

The method for determining alpha cellulose was TAPPI Standard T 203 m 44 which applies to chemical pulps. In this case, it was applied to the prepared holocellulose fraction of the wood which had been dried at 103° C. for about 2½ hours.

In the chemical analyses, instead of testing two samples from the same source simultaneously, one sample of the 4-years' growth before the time of plot treatment was run at the same time as one from the 4-years' growth after treatment. This type of matching was thought to be preferable to the usual duplicate runs on the same sample that subject the separate samples to possible variations in experimental conditions which might obliterate the differences between the two growth periods. The samples were placed in the apparatus at random to prevent possible effects of one piece of equipment always being used with samples of one source class. The several types of analyses produced consistent results associated with either the growth period before plot treatment or after treatment. Without pairing, such differences might be justifiably ascribed to chance error —or the differences might be lost in the pooling of data of a limited number of samples.

Results

The results of the physical and chemical measurements are presented in Tables 1 to 3. Each entry is the average of four trees from the plot and represents the wood formed in the periods before and after the plot treatment as indicated by the column headings.

The plot data for each kind of measurement and analysis were subjected to the "t" test as it applies to significance of difference between means on paired data—in this case before and after treatment. The degree of significance is reported at three levels: 90 percent, 95 percent, and 99 percent.

The "t" test gives an indication of the reliability of the differences between the experimental data for the wood formed on the same trees before as compared to after the fertilizing and thinning. The untreated trees on the control plot provide a check and a basis of comparison over the same periods especially for effects caused by fac-

TABLE 1. Major constituents of wood of young Douglas-fir, in percent,[1] before and after thinning and fertilization. Four years of growth for each period.

Plot number and treatment	Lignin			Holocellulose			Alpha-cellulose			Ash		
	Before treatment	After treatment	Difference[2]	Before treatment	After treatment	Difference	Before treatment	After treatment	Difference	Before treatment	After treatment	Difference
	Percent			*Percent*			*Percent*			*Percent*		
1S control	23.7	23.7	.0	74.5	74.3	— .2	52.8	52.2	— .6*	0.17	0.20	+.03†
2S thinned	23.8	23.6	—.2	75.2	74.6	— .6	52.5	51.7	— .8‡	0.17	0.21	+.04‡
1N fertilized	24.3	24.6	+.3	73.7	72.4	—1.3*	51.0	50.1	— .9*	0.18	0.22	+.03†
2N fertilized and thinned	23.4	23.6	+.2*	75.4	74.5	— .9‡	53.9	52.3	—1.6‡	0.17	0.20	+.03†

[1]Percentages based on oven-dry weights of untreated wood samples.

[2]Each value is the difference between the means—after treatment minus before treatment. A significant difference at the 90% level of confidence is indicated by *; at the 95% level by †; and highly significant, 99% level, by ‡.

tors other than thinning and fertilization. The degree of variation in the response of individual trees to treatment will be reflected in the levels of significance that are obtained. Also, the size of the differences between the data of the 4-year growth peritreatments, as reported in the tables, should be used as an additional guide to judge the importance of any treatment or the combination of treatments. An analysis of variance also was employed on the differences between the data of the 4-year growth periods of the trees, averaging the effects of treatments on a pooled variance basis. The conclusions confirm what can also be deduced from consideration of the degree of significance between the means before and after treatment within the plot and of the magnitude of the differences from one plot to the next.[1]

The first obvious conclusion from the data in Table 1 is that relatively few kinds of chemical analyses were significantly different for the two 4-year growth periods. The trees from the fertilized-and-thinned plot showed a small but significant decrease in the percentage of holocellulose compared to the wood formed prior to the experiment. The plot that was fertilized only, showed an uncertain decrease.

The alpha-cellulose content of the wood formed after plot treatment was lower for all plots than that formed prior to treatment. The degree of significance of the difference between the means for each plot is shown in Table 1. The greatest decrease of alpha-cellulose (1.6 percent) occurred in the plot that was thinned and fertilized. There was no clear-cut effect of thinning alone. Fertilization had the greater effect and there was a tendency toward a greater decrease with the combination treatment as indicated by analysis of variance.

It should be noted that the actual percent of alpha-cellulose of the wood formed after thinning and fertilization (Plot 2N) was as high or higher than that of other plots. This is so because on this plot, the wood of the inner period was initially higher in cellulose averages than that of the other plots for the same period. This indicates again that the differences between the results on the wood formed before and after treatment are a proper measure for com-

[1]Replication of plots was not possible on this established area. However, the four tenth-acre plots were from a single acre which had been selected for uniform conditions.

paring treatment effects and minimizing inherent differences between trees and initial conditions of the plots.

The lignin content was practically the same regardless of the kind of plot treatment. The differences between the means for the periods before and after treatment are so small that even with some significance indicated for one of the plots there is no real importance attached to the variation in lignin content in this sampling.

Considering the data of Tables 1 and 2 it seems clear that if the decrease in alpha-cellulose is real, it is associated with a de-

TABLE 2. Extractives in wood of young Douglas-fir, in percent,[1] before and after thinning and fertilization. Four years of growth for each period. The samples were extracted in the order listed.

Plot number and treatment	Ether extractives			Alcohol-benzene extractives			Hot water extractives			Total extractives		
	Before treatment	After treatment	Difference[2]	Before treatment	After treatment	Difference	Before treatment	After treatment	Difference	Before treatment	After treatment	Difference
	Percent			*Percent*			*Percent*			*Percent*		
1S Control	0.73	0.63	—.10	0.72	1.05	+.33‡	1.33	1.35	+.02	2.77	2.96	+.19*
2S Thinned	0.79	0.66	—.13*	0.78	1.01	+.23†	1.20	1.27	+.07	2.70	2.94	+.24
1N Fertilized	0.76	0.90	+.14	0.71	1.07	+.36‡	1.09	1.14	+.05	2.56	3.11	+.55‡
2N Fertilized and thinned	0.75	0.85	+.10	0.79	1.21	+.42‡	0.99	0.77	—.22	2.53	2.84	+.31†

[1]Percentages based on oven-dry weights of untreated wood samples.

[2]Each value is the difference between the means—after treatment minus before treatment. A significant difference at the 90% level of confidence is indicated by *; at the 95% level by †; and highly significant, 99% level, by ‡.

TABLE 3. Diameter growth, percent summerwood, and specific gravity of young Douglas-fir before and after treatment. Four years of growth for each period.

Plot number and treatment	Diameter growth in inches			Percent of summerwood			Specific gravity (green vol.—o. d. wt.)		
	Before treatment	After treatment	Difference[1]	Before treatment	After treatment	Difference	Before treatment	After treatment	Difference
1S Control	0.46	0.36	—.10†	39	37	— 2	0.521	0.514	—.007
2S Thinned	.048	0.40	—.08‡	36	32	— 4	0.500	0.504	+.004
1N Fertilized	0.56	0.56	.00[2]	32	31	— 1	0.450	0.413	—.037†
2N Fertilized and thinned	0.46	0.64	+.18‡	40	29	—11†	0.523	0.438	—.085‡

[1]Each value is the difference between the means—after treatment minus before treament. A significant difference at the 90% level of confidence is indicated by *; at the 95% level by †; and highly significant, 99% level by ‡.

[2]Although there is no change in Plot 1N it is apparent that the normal falling off of diameter growth with age, as reflected in the control plot, has been prevented by fertilization. Statistical verification was made by the analysis of variance of the differences—before and after treatment—for all 16 trees. The analysis indicated a significant growth response due to fertilization independent of thinning effects and control.

crease in the amount of holocellulose due to fertilizing and thinning rather than a change in the percentage of other constituents such as lignin and extractives.

The ash analyses showed very small but consistent differences between the means of the two growth periods. The slightly higher ash content of the wood formed after treatment is associated with the untreated plot as well as with thinning or fertilization; therefore plot treatments cannot be the causative factor. The differences between the percent ash of the outer and inner samples were only 0.03 to 0.04 percent regardless of plot treatment. It appears that this small increase is associated with position in sapwood or with age. The color of the ash of the outer wood was generally a tan, whereas the color of the ash of the inner fraction was usually gray. The ash was not analyzed for differences in composition.

In only two plots—fertilized, and fertilized and thinned—were there changes in total extractives, after plot treament, that were significant at the confidence level of 95 percent or better (Table 2). The maximum difference was 0.55 percent, in the fertilized plot; in the other plots the difference was 0.3 percent or less. The tendency toward greater total extractives in the last four rings seems to be due to the larger amounts of alcohol-benzene extractives in that portion because a consistent and significant difference is indicated for each of the four plots. The differences ranged from 0.23 percent to 0.42 percent. The data on alcohol-benzene extractives are similar to those of the ash analyses in that the greater quantity found in the outer rings is not confined to plots that had received treatment. The highest alcohol-extractive content and the greatest change were in the fertilized-and-thinned plot and the smallest content and change were in the thinned plot. This argues against the possibility of a shock effect of thinning. Comparing the differences between the treatment means for the 4 plots, it is concluded that the increased amount of alcohol-benzene solubles found in the outer portions was due in part to position in the sapwood and that additional amounts were associated primarily with fertilization. There was a tendency toward somewhat greater effect in combination with thinning. Kurth's data (1948) on Douglas-fir show greater amounts of ether and alcohol extractives but his samples were on wood from older trees, included some heartwood, were from a different geographical area and, therefore, probably from a completely different site.

The amounts of ether extractives and hot-water extractives before and after plot treatment were not significantly different for any of the plots. Neither treatment nor position in the sapwood had any apparent effect on these constituents.

In the control plot, the diameter growth was 22 percent less during the last 4 years than during the previous 4 years (Table 3). Aside from a normal decrease expected due to competition there was an unusually dry year in 1952 which may have contributed to the decrease. In the thinned plot, the growth rate before thinning was almost the same as for the control plot; but the growth after treatment (thinning) did not decrease as much (17 percent) as in the control plot (22 percent). Fertilizing appeared to maintain the prior growth rate in the unthinned stand. Fertilizing and thinning combined gave a greater growth rate than either treatment singly and was 39 percent greater than the diameter growth of the same trees for the 4 years prior to treatment of the plot. In comparison to the control plot and the thinned plot, which also had the same diameter growth for the period prior to treatment, the increase in the growth of these trees on the fertilized-and-thinned plot is all the more striking. The effect of thinning on growth was significant but there was no significant interaction with fertilization, therefore, no enhancement beyond the normal contributions from both factors.

The percent of summerwood in the two growth periods, before and after treatment, was about the same in all plots except the

thinned and fertilized. In this case, the percentage decreased (significant at 95 percent level) from 40 percent before treatment to 29 percent after treatment. One reason for this may be the faster growth rate after plot treatment.

The specific gravity of the wood formed before and after treatment was the same for the control plot and for the thinned plot (Table 3). Fertilization caused a decrease of 8 percent in specific gravity, and fertilization plus thinning caused a decrease of 16 percent. The high level of statistical significance coupled with the percentage decrease gives much more importance to the results of the combination treatment than to the fertilization only.

An association is indicated between specific gravity and the percent of summerwood in the rings. The fertilized-and-thinned plot was the only one which showed a decrease, from previously formed wood, both in specific gravity and percent summerwood. As previously noted, the decrease in specific gravity in this plot was much more than in the plot fertilized only, which showed no significant change in percent summerwood.

The average summative analysis values by plots for extractives, lignin, and holocellulose (corrected for residual lignin of 0.5 percent) range from 100 percent to 101 percent for each of the 4 plots which, considering the sequence of analyses, is within acceptable limits of departure from the theoretical 100 percent. It also indicates that no set of experimental data is likely to be far from the true values.

Discussion

Except for special situations, the experiment indicates that the cellulose content is the chemical factor that warrants further study with more samples as well as more widespread sampling of different areas and sites. Reductions of one percent or more of holocellulose and alpha-cellulose could assume importance in the production costs of the pulp and chemical utilization industries. Likewise, wood chips of low specific gravity give less cellulose yield per unit of space and per unit of cooking chemicals than chips of higher density—other things being equal. Therefore, it becomes economically important to know if the wood from treated forests will produce as much usable cellulose at a comparable cost of pulping as wood from untreated forests.

Wilde *et al.* (1951) found that even in areas of faster growth and lower specific gravity of wood (jack pine) the yield of alpha-cellulose per acre was much greater than on other areas. They also found that the yield of alpha-cellulose per cord was 8 percent greater in wood from a fertile site than in wood from a poor site. (However, another poor site also gave a high yield of alpha-cellulose per cord and the highest yield on a weight-of-wood basis.) The question arises whether different inherent characteristics of trees are involved or if the site conditions are the direct cause of these differences. In the present study of Douglas-fir, a comparison of wood formed before and after treatment of the stand shows that part of the variation between plots is caused not by the changing of site quality but rather by inherent differences between the trees and the plots. In contrast to the study mentioned above, the content of alpha-cellulose in this study was somewhat lower as a result of better growing conditions for the same trees on the same plots.

The practical aspect is that an increased rate of wood production per acre on a poor site and a lower cost per unit of volume may offset a small difference in percent of cellulose, a lower specific gravity of wood, and a slightly higher pulping cost per ton of pulp. In addition, the greater volume produced is desirable as long as mechanical and physical properties are not impaired to the extent that marketability is seriously affected.

The growth rate during the final 4 years of the trees used in this study was in the same order as that found by Shareeff (1955) on a more intensive growth study on the same areas. The order in both

studies was: control < thinned < fertilized < thinned and fertilized. Data on the 50 largest trees in each 1/10-acre plot (Shareeff, 1955; Gessel and Shareeff, 1957) show that the volume of total-stem growth on the fertilized plot was double that on the control plot. The increase on the thinned and fertilized plot was 66 percent more than the control value (Shareeff, 1955). Computations on the selected co-dominant trees used in this study show increases of approximately 60 percent and 80 percent for the respective plots based on an average diameter of 4 in. and volume increment for a cylinder of unit length. Considering the greater spread of tree sizes in the 50 largest trees the difference in expressing growth volume, and the greater accuracy obtainable by a larger sample, the agreement between the two experiments is good.

If the annual increment per acre for the high Site V for the 500 largest trees in that acre can be increased (Shareeff, 1955) from 82 cu. ft. (control plot) to 108 cu. ft. (thinned) to 122 cu. ft. (fertilized) to 136 cu. ft. (fertilized and thinned), then reductions of specific gravity of 10 to 15 percent should be tolerable from the standpoint of fiber production. No attempt was made here, nor in the other studies on these areas, to determine the costs of fertilizing and thinning, but on the basis of the increments of the first and last plots just mentioned and applying the correction for specific gravity change found in this experiment, the periodic annual fiber yield per acre was 3,700 lbs. for the fertilized-and-thinned plot and 2,650 lbs. for the control plot, a gain of 1,050 lbs. of fiber per acre per year. This indicates that moderate reductions in specific gravity can be disregarded because of the increase in annual increment.

Finally, it should be kept in mind that work reported in this paper was necessarily limited to one small forest area of quite uniform conditions. Further studies on the effects of fertilizing and thinning a stand upon the character of the wood are obviously very desirable.

Summary

The effects of fertilization and thinning on wood formed over a 4-year growth period on a 30-year-old Douglas-fir stand (high Site V) were compared to the wood formed on the same trees in the 4 years before treatment. Four 1/10-acre plots were used — control, thinned, fertilized, and thinned and fertilized. Four average co-dominant trees were selected from each of the 4 plots. The tree sections used for study were taken at breast height.

The wood formed in the two growth periods, before and after plot treatment, was analyzed for lignin, holocellulose, alpha-cellulose, ash, and three classes of extractives—hot water, alcohol-benzene, and ether. There was little or no significant difference in most cases between the analyses of the wood formed before or after plot treatment. Slightly lower holocellulose and alpha-cellulose values were found in the wood formed after fertilization. Thinning caused some tendency toward reduced cellulose content compared to the wood formed before thinning on the same trees, but thinning and fertilization combined gave the greatest reduction. In all plots, control and treated, ash was slightly but not importantly higher in the outer rings than in the growth prior to the last 4 years. The same was true of the alcohol-benzene extractives. Ether solubles and hot-water solubles showed no change with either radial position or plot treatment.

Growth rate was greatest in the fertilized-and-thinned stand, second in the fertilized stand, third in the thinned stand, and least in the control. The results on growth are compared to data obtained by others which represent measurement of volume increment of all trees in the plots.

The percent of summerwood decreased significantly in one case — after thinning and fertilizing. Specific gravity decreased following fertilization, more so with the combination of thinning and fertilizing. The increased volume increment obtained from fertilizing and thinning had much more

weight of fiber (dry basis) than untreated stands even after allowance for a decrease in specific gravity.

There is a need for more studies on the effects of fertilization and thinning on the cellulose content, growth rate, and specific gravity using more samples and trees from different geographical areas, age classes, and site classes.

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Tracheid Length Variation and Inheritance In Slash and Loblolly Pine

BY
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CONIFER TRACHEID LENGTH has been a subject of investigation throughout the world for over 80 years. Spurr and Hyvarinen (1954) published a fairly comprehensive review of the literature on wood fiber dimensions as related to position in the tree. Most of the investigations were made for the purpose of (1) continuation of Sanio's work on distribution of fiber length in the stem, (2) variation within tissues such as springwood and summerwood, or (3) effect of growth rate on fiber length. Conifer tracheid dimensions and structure are closely related to properties of wood quality such as strength, shrinkage, density, and pulp yield (Mitchell, 1956). Current interest in the selection of superior trees for breeding purposes has given impetus to the study of the hereditary variation in the anatomical features such as tracheid length, proportion of summerwood, specific gravity, and fibril angle. The objective of this study was to determine to what extent the tracheid length in slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.) is modified by breeding.

Procedures

Wood samples of parents and their open- and cross-pollinated progeny were obtained from the forests and out-plantings at the Ida Cason Callaway Foundation at Hamilton, Georgia. Most of the progeny stock had been propagated by the junior author while in the employ of the Foundation from 1950 to 1954.

In other studies by Carnes (1957) and Greene (1956), it was found that first ring tracheid length in stem-branch pairs was highly correlated for slash pine ($r = 0.7313$) and loblolly pine ($r = 0.646$ and $r = 0.7313$). In two 24-year-old loblolly pines, there was only a small variation in first ring tracheid length with height in stem, the total range being only 1.38 to 1.84 mm. These data showed that it is feasible to use branch tracheids for comparative purposes. The use of branch samples also prevented serious injury to the parents and their progeny. Tracheid length measurements were made of the wood in the first ring from the pith of the branches. Single branches were taken from the topmost whorl of 7 slash pine and 3 loblolly pine parent trees and 10 open-pollinated progeny of each parent. Single branches were also taken from the topmost whorls of 10 cross-pollinated progeny of each of the following crosses: (1) 1 slash × slash, (2) 2 loblolly × loblolly, and (3) 4 slash × loblolly. Wood maceration and tracheid measurements were made according to the method described by Jackson and Greene (1957 a, b).

The authors are Professor of Silviculture and Assistant Professor of Forestry, respectively, University of Georgia. The work was carried on in cooperation with the College Experiment Station. Journal Paper No. 63, College Experiment Station.

Results

Data on branch first-ring tracheid length variation in parents and their progeny are shown graphically in Figure 1. In the slash pine open-pollinated series, the tracheids of the progeny were significantly (at 5 percent level) shorter than those of the parents in 6 of the 7 parent-progeny combinations. An analysis of the data revealed that the progeny from parents with relatively long tracheids had relatively longer tracheids than the progeny from parents with relatively short tracheids. Of the possible 21 comparisons of parents and progeny, the parents with the longer tracheids had progeny with longer tracheids in 14 or 67 percent of the combinations. For one of the parents that had the longest tracheids, the progeny had longer tracheids than 5 of the 6 comparisons. Similar results were obtained for 2 of the 3 loblolly pine combinations used in the study.

Tracheid length varied quite widely in the open-pollinated series with a range of 1.09 to 1.57 mm. between individual slash pine parent trees. Range among the 3 loblolly pine parents was 1.10 to 1.55 mm. Tracheid length of the 2 groups of open-pollinated progeny varied from 1.05 to 1.27 mm. This difference of 0.22 mm. is about half of that (0.48 mm.) of the maternal parents and demonstrates the "leveling" effect of open pollination.

In the cross-pollination series, the average tracheid length of the progeny in 5 of the 7 combinations of both species was intermediate to that of the two parents, equal to the female parent in one and the male in one of the crosses. Furthermore, in all except one of the crosses, the tracheid length of the progeny was much closer to the tracheid length of the female than the male parent. An analysis of the data revealed that the tracheid length of the progeny in 83 percent of the possible combinations of parents and progeny was influenced more by the female than the male parent. The tracheid length between all parents varied widely from 1.09 to 1.55 mm. Tracheid length of the progeny from all crosses of both species varied from 1.13 to 1.33 mm. with a difference of 0.20 mm. which is about half of that (0.46 mm.) of the parents of both species.

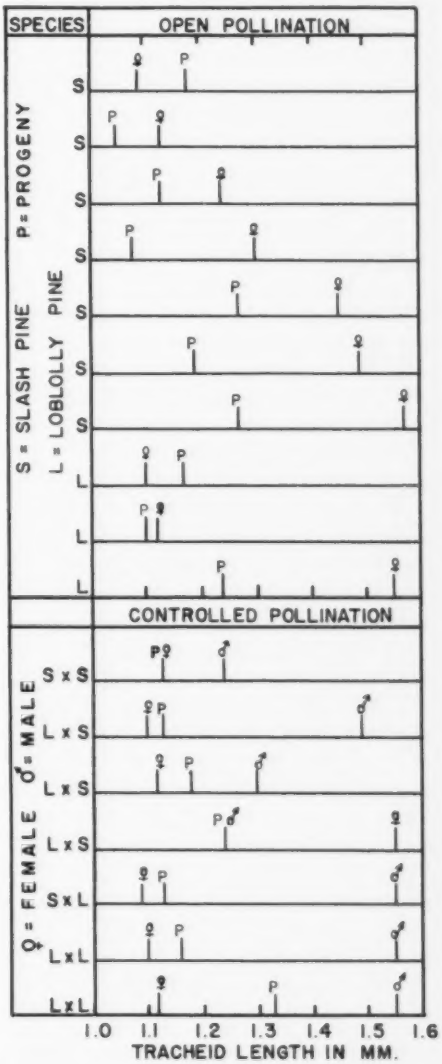

FIGURE 1. *Pattern of tracheid length in slash and loblolly pine parents and their open- and cross-pollinated progeny. The cross pollinations are shown as mother tree on male tree.*

Conclusions

There is considerable variation in the length of tracheids within an individual tree as well as between parent trees in a stand. Wardrop and Dadswell (1953) in Australia found that when the first ring tracheids were relatively long they remained longer through successive rings in comparison with stems with shorter tracheids. They suggested the possibility of breeding for long initial tracheid length. According to the results of this investigation, the tracheid length of slash pine and loblolly pine is quite variable between trees and is modified by hereditary factors. On the basis of these results it should be feasible to breed pines for long or short tracheids.

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Absorption and Translocation of 2, 4, 5-trichlorophenoxyacetic Acid Derivatives in Quaking Aspen

BY
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APPLICATION OF PHYTOTOXIC CHEMICALS has become an effective tool for chemical bark removal of pulpwood and for the control of undesirable woody plants. Recent studies (Shiue, 1957) indicate that the bark of certain species, particularly quaking aspen (*Populus tremuloides* Michx.) may be loosened by external application of oil solutions of 2,4,5-trichlorophenoxyacetic acid derivatives. This observation brings into consideration not only the question of translocation of the chemical within the stem but also more directly the mechanism of penetration of the chemical through the bark. Studies by Coulter (1951), Meador and Fisher (1953) and Hay (1956a, 1956b) indicate that the chlorophenoxyacetic acid derivatives when applied externally to the bark of some woody plants move predominantly upward and that the downward movement within the plant is either absent or limited to a short distance. The course by which these derivatives penetrate the bark of woody plants and are translocated within the stem has not been reported. The objectives of the present study were, therefore, to determine how chlorophenoxyacetic acid derivatives are absorbed by quaking aspen when applied externally to the bark, and by what course they are translocated within the trees. Different types of chemicals and various methods of application were compared.

Methods and Results

Absorption through bark. Since diesel oil has been widely used as the carrier in application of chlorophenxyacetic acid derivatives, the translocation of the chemical was assumed to follow the course taken by the diesel oil. To determine this movement, the carrier was colored with an oil-soluble anilin red. External application of the colored hormone solution to the bark led to the appearance of stained spots on the inner bark and wood, thus defining the actual point of entrance of the material into the stem.

When smooth-barked aspen trees (Kaufert, 1937) were treated with a solution of butoxy ethyl ester of 2,4,5-T in colored diesel oil during the period of rapid growth, red spots appeared in the inner bark at the site of treatment after three days. These spots were coincident with the bark lenticels as illustrated in Figure 1. On the sixth

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day the red spots had extended radially into the sapwood with a subsequent upward movement. After 12 days the sapwood, but not the bark, in the upper region of the stem showed very light red stripes extending to the top and the terminal leaves started blackening and wilting (Fig. 2).

The results from treatment of rough-barked aspen trees differed only in that the initial stained area in the inner bark and sapwood appeared as a longitudinal stripe corresponding with the longitudinal bark fissures.

In order to compare the reaction to the chemical of different formulations following various methods of application, 12 two-year-old potted aspen plants were divided into four groups of three plants each. In each group, a plant was randomly assigned to one of the following treatments: (1) 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), (2) butoxy ethyl ester of 2,4,5-T, and (3) diesel oil only. The chemicals were dissolved in diesel oil at a concentration of 2.4 grams in 100 cc., and applied outside the bark as a wet band 1-inch wide located 3 inches above the ground line during the period of rapid growth.

The plants treated with 2,4,5-T acid remained in normal condition for about four weeks. At the end of six weeks the terminal bud started to unfold and produced new leaves of distorted form. This distortion may be the result of uneven distribution of the growth-stimulating 2,4,5-T acid within the leaf. Plants treated with the butoxy ethyl ester of 2,4,5-T were completely killed within six weeks. The ester form of 2,4,5-T was, therefore, apparently more effectively absorbed through the bark of the aspen plants than was the pure acid. Since the control plants, which were treated with diesel oil alone, grew normally, all the response shown in treated plants may be attributed to the action of hormone chemicals for which the diesel oil serves as a carrier.

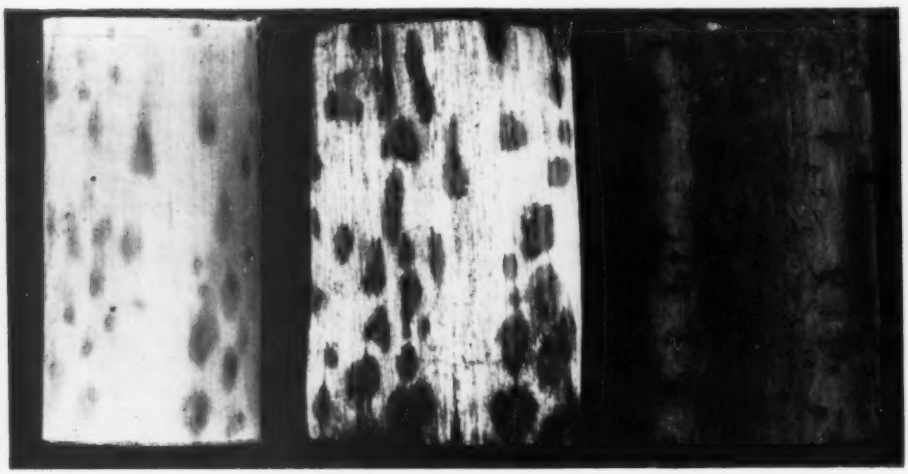

FIGURE 1. *Stained areas on sapwood and inner bark showing coincidence with locations of lenticels on smooth bark where chemical penetrated. Sample taken 6 days after treatment. Left: Sapwood with light-red spots. The less distinct areas above each spot indicate upward vertical translocation or diffusion. Center: Inner bark with corresponding red spots. Right: Note the perfect coincidence of the locations of lenticels on the smooth bark with the red spots on the sapwood and inner bark.*

Translocation. The aspen leaf is so sensitive in its response to minute quantities of chlorophenoxyacetic acid derivatives that the extent of translocation of such chemicals can be observed without difficulty. One of four groups, each composed of five young aspen plants (approximately five years old), was randomly assigned to one of the following treatments:

1. One-inch strip girdle, 2 feet above the ground line.
2. Intact bark sprayed with butoxy ethyl ester of 2,4,5-T in diesel oil, 2.4 grams in 100 cc., as a wet band 3 inches wide and 2 feet above the ground line.
3. One-inch strip girdle, sprayed with the butoxy ethyl ester of 2,4,5-T in diesel oil below the girdle.
4. One-inch strip girdle, sprayed with the butoxy ethyl ester of 2,4,5-T in diesel oil above the girdle.

Girdling did not affect the growth of the plant during the first season except for the appearance of swelling and callus tissue directly above the girdle (Fig. 3-I). Within three weeks after the ungirdled aspen plants were treated with butoxy ethyl ester of 2,4,5-T the plants were killed both above and below the point of treatment (Fig. 3-II). When a girdle was placed above the zone of treatment, effective killing was obtained both above and below the girdle (Fig. 3-III). This shows that the chemical passed upward through the xylem in lethal concentrations even though a complete girdle was made above the place of application. Figure 3-IV shows an aspen plant that had been girdled and treated above the girdle with butoxy ethyl ester of 2,4,5-T. In this case killing was observed above the girdle, but foliage below the girdle was not affected. Removal of the bark in girdling thus inhibited the downward translocation of lethal quantities of the chemicals.

The tangential translocation within the aspen tree was shown to be rather limited. When one half of the circumference of a tree was treated with butoxy ethyl ester of 2,4,5-T, only the half of the crown on the side corresponding to the treated section of bark was killed. This effect continued for an entire growing season.

FIGURE 2. *Illustration of upward movement of chemicals through the sapwood. Sample taken 12 days after treatment at a position 6 feet above the point of treatment. Left: Sapwood with light-red stripes from the bottom to the top. Right: Inside of inner bark, showing no staining from the red dye.*

In order to test the effect of emulsifying additives on the absorption and translocation, the treatments were compared on two-year-old aspen plants as follows:

1. Butoxy ethyl ester of 2,4,5-T in diesel oil placed on the intact stem.
2. Butoxy ethyl ester of 2,4,5-T in diesel oil applied to freshly exposed wood surface of the stem.
3. A water emulsion of butoxy ethyl ester of 2,4,5-T, using Product "A" from a solvent free petroleum ether extractive of aspen bark (Hossfeld, 1958) as the emulsifying agent, ap-

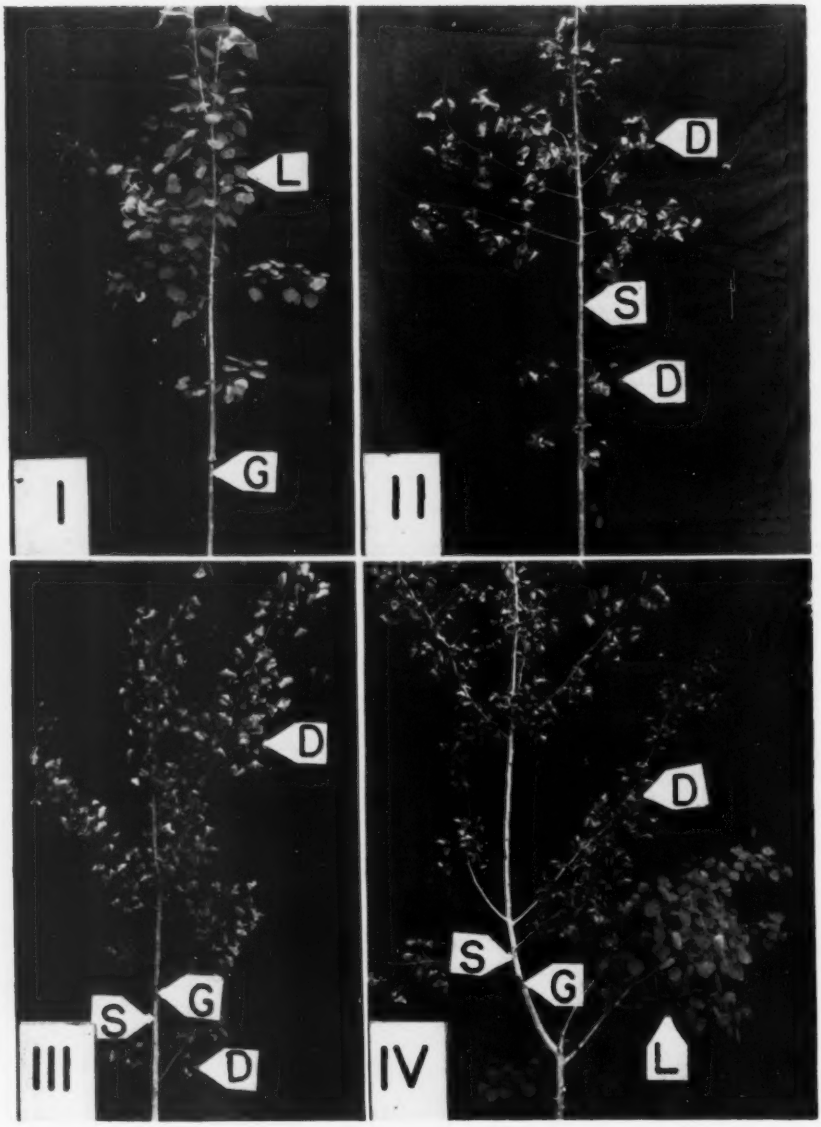

FIGURE 3. *Typical responses of aspen saplings to various treatments. D, dead foliage. L, living foliage. G, position of girdle. S, position of spray.*

I. The plant girdled at G remained normal for three months after girdling except for the growth and the swelling of the bark above the girdle.

II. The plant sprayed at S with ester of 2,4,5-T was killed.

III. The plant sprayed with ester of 2,4,5-T below point of girdling was killed.

IV. The plant stem sprayed with ester of 2,4,5-T above point of girdling was killed, but the limbs and twigs below the girdle were still alive.

plied to the freshly exposed wood surface of the stem.

The concentration of chemical was 2.4 grams in 100 cc. of solvent. The chemical was absorbed on cheese cloth strips, the strips wrapped on the stem at the position of treatment, and covered with a plastic sheet to protect from rain and rapid evaporation. Response of aspen plants to these treatments was observed weekly.

Application of the butoxy ethyl ester of 2,4,5-T directly to the intact stem killed the plant. However, when the butoxy ethyl ester of 2,4,5-T was applied to the freshly exposed wood the plant remained alive for a full growing season. When the pure ester was emulsified with an aspen bark extractive and then applied to a freshly girdled wood surface, the plant was killed. Since the water-insoluble ester form of 2,4,5 T did not kill the plant when it was placed directly in the transpiration stream, but did kill the plant after it was emulsified with the aspen bark extractive, it is inferred that some of the chemical components of aspen bark are responsible for the peculiar sensitivity of aspen to the pure ester form of 2,4,5-T. When free-hand sections of aspen bark (50μ) were cut and stained with dilute iodine solution, many blue granular structures were found in ray cells, phloem parenchyma, and phelloderm. These blue granules did not change their color when heated. According to Johansen (1940), this test indicates the probable presence of saponins in the aspen bark. Since saponins are emulsifying agents, they may, if present, play an important role in the action of the pure ester of 2,4,5-T on aspen.

Summary

When the butoxy ethyl ester of 2,4,5-T in diesel oil was applied externally to the bark of aspen plants, the chemical penetrated the protective tissue through the fissures and lenticels, and was absorbed by the living tissues of the bark from which it was translocated radially into the sapwood, thence upward in the transpiration stream in the xylem. The downward movement took place within the bark. The tangential translocation of chemical was negligible.

When the pure ester form of 2,4,5-T was applied to the exposed wood of a freshly strip girdled stem, the chemical was not effectively translocated in the transpiration stream and there was no evidence of lethal effect. However, the chemical killed the aspen plant when it was applied to the stem outside the bark. Application of 2,4,5-T ester emulsified with an aspen bark extractive to a freshly girdled wood surface also effectively killed the plant. Components of aspen bark extractive, probably in the nature of saponins, appear to play an important role in the effective absorption and translocation of chemical within the plant. The presence of these materials in aspen bark may explain the unusual sensitivity of the plant to bark application of the pure ester form of 2,4,5-T.

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Principles of Plant Pathology

By E. C. Stakman and J. George Harrar. The Ronald Press Company, New York. 581 pp., illus. 1957. $8.00.

Review by J. S. Boyce
Yale University

This book on plant pathology differs markedly from the many that have preceded it. It is not a manual. It is not for the practitioner. It is not a book in which to look up a specific disease to determine its distribution, economic importance, symptoms, cause, and control. Rather it is a stimulating volume on the basic principles of plant pathology.

Of the eighteen chapters those on the genetics of plant pathogens, the effect of environment and nutrition on disease development, quarantines, eradication campaigns and international plant protection, and resistant varieties were especially rewarding to the reviewer. The authors point out that quarantine and eradication programs, because action is taken after the initial damage has been done, are always an admission that science has not found a satisfactory way to cope with certain pathogens.

The two chapters on the genetics of plant pathogens and on resistant varieties can well be read together. The development of varieties resistant to disease is probably the most valuable single control of plant diseases for the future, but the development of new pathogenic strains by mutation and the possible susceptibility of new varieties to other diseases are phenomena that make this method less than certain. Furthermore, developing resistant varieties may be so time consuming that a crop may be destroyed economically before resistant varieties can be developed, i.e. the American chestnut attacked by chestnut blight. Furthermore, the plural is important. Dependence on a single resistant variety is highly hazardous. In addition, the cost of developing resistant varieties may in the long run exceed the cost of control by chemicals. The possibility that nature can breed new pathogens as fast or faster than man can breed resistant varieties is particularly disturbing to a forester, since several to many decades will usually be needed to develop a resistant variety of a tree.

There are certain omissions. The increasingly important subject of air pollution is combined with soil contamination and both are dismissed with a few lines. Under important international diseases, chestnut blight, Dutch elm disease, and white pine blister rust are not mentioned. There are no citations in the text to the list of selected references at the end of each chapter, which makes it difficult for the reader to pursue any particular subject further.

This book is essential reading for every plant pathologist. It is the first devoted to an overall evaluation of the many factors that affect the development of diseases and their control. It is a successful attempt to establish a scientific rather than an empirical basis for plant pathology.

Genotypic Variation in the Time of Cessation Of Height Growth in Douglas-Fir

BY
HELGE IRGENS-MOLLER

In 1898 Ortenblad in Sweden observed that Scotch pine (*Pinus silvestris* L.) from northern Sweden stopped height growth in August when planted near Stockholm, Sweden, whereas plants from southern Sweden, planted adjacent to the former, continued growth until fall frosts killed the terminal shoots. Ortenblad ascribed these differences to hereditary adaptations to the length of frost-free periods in northern and southern Sweden (Bornebusch, 1935).

In 1913 Engler showed that such differences among altitudinal ecotypes of Norway Spruce (*Picea abies* (L.) Karst.) are of a genetic nature. Genetic diversity with regard to the time of cessation of height growth has been described in a number of other forest tree species (Cieslar, 1895; Engler, 1908; Kriebel, 1957; Langlet, 1936; Pauley and Perry, 1954; Schott, 1907; Vaartaja, 1957).

The present investigation represents an effort to determine the genotypic variation in time of cessation of height growth among seedlings of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) of known origin when grown in a uniform environment at Corvallis, Oregon. An attempt is also made to determine genotypic variations in response to various photoperiods.

Methods and Results

During the fall of 1956 seeds[1] of Douglas-fir were obtained from the areas shown in Figure 1 as follows:

1. Browder Creek, Santiam Pass, Oregon, at 4000 feet elevation and with a frost-free period of less than 90 days (U. S. Dept. Agric. 1941). Seed from this area were collected from three single trees growing adjacent to each other.

2. Detroit, Oregon, at 3600 feet elevation with a frost-free period of less than 90 days. This collection is a stand collection as are all the following collections.

3. Eddyville, Oregon, at 100 feet elevation with a frost-free period of more than 200 days.

4. Salmon Arm, southern interior British Columbia, at 1900-2100 feet elevation with a frost-free period of less than 90 days (Kendrew, 1953).

5. Qualicum, Nanaimo, and Alberni on southern Vancouver Island, B. C. at elevations ranging from 180-690 feet and with a frost-free period of more than 200 days.

Seed from these localities were sown in

[1]The author is indebted to Manning Seed Company, Seattle, Washington for seed from many of the localities mentioned in this paper.

The author is Assistant Professor, School of Forestry, Oregon State College. This paper is part of a thesis submitted to the Graduate School of Oregon State College in partial fulfillment of the requirements for a Ph.D. degree in Botany. The project has been supported substantially by a grant from the Forest Genetics Research Foundation.

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February, 1957 in the greenhouse in 4-inch pots. After germination the seedlings were thinned to two to three seedlings per pot. On April 2 the plants were moved out-of-doors and placed in cold-frames. Weekly height measurements were started on July 30. A piece of heavy galvanized wire was placed along each of 20 randomly selected plants from each source. The height of each plant above the cotyledonary node was marked with pencil on the wire each week. The week in which height growth ceased was defined as the week in which no increase in height from the previous week could be detected.

The height growth in young Douglas-fir seedlings does not occur continuously during the season as in certain deciduous forest tree species (e.g., poplar and birch) but in periods of internode extension followed by periods characterized by the formation of a terminal bud. The period of growth consists only of extension of internode-primordia already present in the terminal bud.

The plants native to coastal climates (Eddyville, Oregon, and Vancouver Island) stopped height growth one to four weeks later than the plants from interior British Columbia (Salmon Arm) and the high Cascades (Browder Creek). Furthermore, the plants from interior British Columbia and the high Cascades were charac-

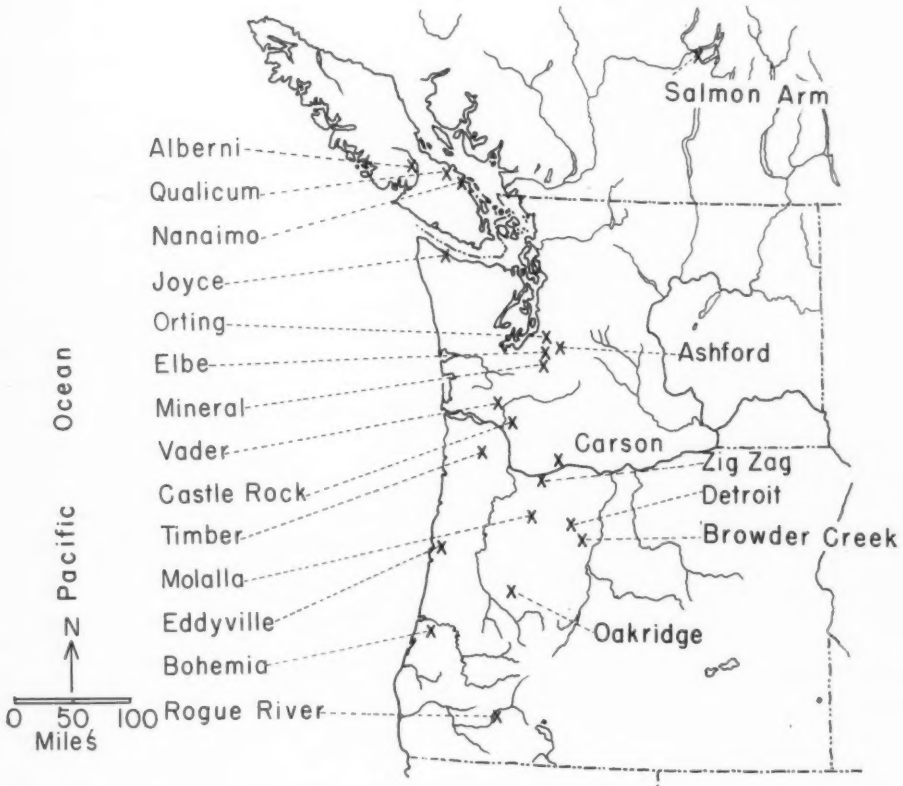

FIGURE 1. *Map of Pacific Northwest showing localities from which seed were obtained.*

terized by a longer period between the first and second period of internode extension than plants from coastal climates. In the latter the periods of internode extension followed each other rapidly and the terminal bud formed between these periods was indistinct, of short duration, and difficult to detect.

The differences in the time of cessation of height growth among the various groups of plants were reflected by the total heights of the seedlings at the end of the growing period. The plants which stopped growth early attained less height than those which continued growth late in the season (Fig. 2). Thus, the plants from Salmon Arm, British Columbia, attained an average height (above the cotyledonary node) of only 22 mm. as compared to 72 mm. (Qualicum), 86 mm. (Nanaimo), and 112 mm. (Alberni) for the plants from Vancouver Island. Similarly, the plants from Browder Creek attained average heights of only 55 mm. (tree #88), 75 mm. (tree #87), and 35 mm. (tree #84) as compared to 151 mm. for the plants from Eddyville.

These differences at Corvallis are in all probability not the same as those between the plants growing in their native habitats.

Differences in time of cessation of height growth can also be detected simply by observations of the percentage of dormant plants at a certain date. Such observations were made on July 8th, 1957, on plants from 20 different sources (Table 1) sown in February 1957 in the greenhouse and placed out-of-doors in cold-frames on April 2. Twenty randomly selected plants from each source were observed as to dormancy, including earlier dormancies (i.e., some of the plants had at this time started a second period of internode extension). The persistence of the bud scales or bud scale scars made such observations relatively easy. All of the plants from interior British Columbia had been dormant once prior to July 8 (Table 1). Similarly, 70 to 80 percent of the plants from the four localities at high elevations near Detroit, Oregon, had been dormant earlier. However, whereas 55 to 90 percent of the plants from Detroit were actively growing on July 8 (i.e., had started a second period of internode extension), only 20 percent of the plants from interior British Columbia were actively growing at that date.

Relatively few of the plants from coastal areas (Vancouver Island) had been dormant prior to July 8 and almost all of them were actively growing. Plants from Vader in southwestern Washington reacted unexpectedly in almost the same way as the plants from high elevations near Detroit, Oregon.

All the above described plants were growing under essentially the same environmental conditions. The observed differences may therefore be ascribed to genetic differences.

Photoperiodic Influences

Seed from seven different localities in the Pacific Northwest (Table 2) were stratified for two weeks at 5°C. and sown on February 26 in pots in the greenhouse.

FIGURE 2. *Comparisons between Douglas-fir seedlings 10-months old of different origins sown February 1957. From left to right: Salmon Arm, British Columbia, 1900-2120 feet; Qualicum, Vancouver Island, 200 feet elevation; Browder Creek, Santiam Pass, Oregon, 4000 feet elevation; and Eddyville, Oregon, 100 feet elevation. For location of seed sources see Figure 1.*

Plants from each source were given each of the following photoperiodic treatments (all light given in addition to normal daylight was given from a 40-watt incandescent bulb suspended three feet above the plants):

1. Eight a.m. to 5 p.m. (9 hours).
2. Eight a.m. to 5 p.m. with a "light-break" from 9 p.m. to 10:30 p.m. (10½ hours).
3. Eight a.m. to 5 p.m. with a "light-break" from 2 a.m. to 3:30 a.m. (10½ hours).
4. Four a.m. to 11 p.m. (19 hours).

On May 25 20 randomly selected plants from each source and treatment were cut off at the soil surface and the number of leaves counted on each plant.

The plants exposed to nine-hour photoperiods (treatment 1) had developed an average number of leaves of only 15 (Table 2). Additional light from 9 p.m. to 10:30 p.m. (treatment 2) increased the average number of leaves to 21. If the additional light was given from 2 a.m. to 3:30 a.m. (treatment 3) the average number of leaves was increased to 25. Thus, although the same total amount of

TABLE 1. Percentage of actively growing plants dormant on July 8 and percentage of plants which had been dormant once or twice prior to July 8, 1957, when grown at Corvallis, Oregon.[1]

Locality	Elevation	Actively growing plants on July 8	Plants which had been dormant once prior to July 8
	Ft.	*Percent*	*Percent*
British Columbia			
Qualicum, Vancouver Island	200	100	10
Nanaimo, Vancouver Island	180-200	100	50
Alberni, Vancouver Island	690	95	35
Salmon Arm	1900-2120	20	100
Washington			
Joyce	280	90	55
Vader	300-400	40	85
Castle Rock	450	90	20
Orting	400-450	100	15
Carson	900-950	95	60
Castle Rock	950-1000	85	45
Elbe	1050-1250	90	40
Castle Rock	1100-1250	90	70
Ashford	1500	95	35
Mineral	1550	85	55
Oregon			
Timber	750-900	100	25
Molalla	750-950	100	5
Detroit	1620-1820	90	70
Detroit	2300-2550	80	80
Detroit	2800-3000	55	70
Detroit	3600	80	80

[1]Based on 20 plants from each locality. For location of seed sources see Figure 1.

TABLE 2. Responses of three-month old Douglas-fir seedlings of different origins when treated with four different photoperiods after germination. Underlined figures denote average number of leaves per seedling. Figures not underlined denote percentage of actively growing plants.

Origin[1]	Treatments 1	2	3	4	Source Averages
Oakridge, Oregon	12.15	21.10	24.50	27.70	21
2500-3500 ft.	5	95	97.5	1000	74
Mineral, Washington	16.70	20.25	27.00	28.35	23
1550 ft.	45	100	100	100	86
Ashford, Washington	18.05	19.20	24.95	25.90	22
1500 ft.	55	85	100	100	85
Elbe, Washington	15.50	26.95	26.60	27.05	24
1050-1250 ft.	70	100	100	100	83
Nanaimo, Vancouver Island	16.00	25.30	26.10	24.30	23
0-500 ft.	82.5	97.5	97.5	100	92
Salmon Arm, B. C.	11.70	20.85	26.20	23.30	21
1900-2120 ft.	0	55	90	87.5	54
Shuswap Lake, B. C.	9.85	16.15	20.15	24.60	18
1000-1500 ft.	0	42.5	50	97.5	54
Treatment Averages	15	21	25	26	—
	34	75	92	98	

[1]For location of seed sources see Figure 1.

light was given in treatments 2 and 3 a greater effect was obtained if the "light break" was given during the latter half of the dark period than during the first half. Long-day treatment increased the average number of leaves to only 26 (treatment 4). A "light-break" during the latter half of the dark period is thus almost as effective as a long photoperiod, indicating that the periodicity rather than the total amount of light is the governing factor. Both the responses to treatments and the sources differ significantly at the 5 percent level.

The plants from interior British Columbia showed the greatest differences between responses to the four photoperiods. Thus, the number of leaves developed under treatment 3 was 224 (Salmon Arm) and 250 (Shuswap Lake) percent greater than those developed under treatment 1, compared to only 150 percent for the plants from Nanaimo, Vancouver Island. The corresponding figures for the remaining sources are: Oakridge, 200; Mineral, 170; Ashford, 143; and Elbe, 174.

The number of leaves per seedling is related to the length of the period of height growth. Only 34 percent of the seedlings exposed to nine hours of light were still growing at the time of sampling compared to 75, 92, and 98 percent in the other three treatments. The complete dormancy of seedlings from the interior of British Columbia on the 9-hour day-length suggests differences with respect to photoperiodic sensitivity (Table 2).

Discussion

Numerous experiments have shown that most forest tree species respond to short days by ceasing height growth (Wareing, 1956). Differences in the time of cessation of height growth have therefore been ascribed to differences in response to the natural decrease in day-length during summer. (Pauley and Perry, 1954). The selective advantage of such a response to decrease in day-length is evident from the fact that day-length is the only environmental factor which changes in a consistent manner during each year, whereas the first killing frost during fall varies widely from year to year (U. S. Dept. Agric., 1941). A high sensitivity to the natural decrease in day-length would appear to be of particular advantage in plants native to areas where the climatic changes from summer to winter are severe and abrupt. The fact that plants native to such areas show the greatest sensitivity to artificially reduced day-length (Table 2) indicates that response to photoperiod is an important component of adaptation to the length of frost-free period.

The ease with which photoperiod may be controlled experimentally provides an excellent opportunity for the study of genotypic variation in a widely distributed species such as Douglas-fir. Future experiments may reveal certain correlations between sensitivity to photoperiod and other characteristics such as drought or frost endurance which are considerably more difficult to determine experimentally.

Conclusion

Genetic diversity exists among Douglas-fir seedlings of different origins with respect to the time of cessation of height growth. The response to the natural decrease in day-length during the summer is an important factor in the adaptation to the length of the frost-free period.

Seedlings of montane or interior origin grew less at Corvallis than those of coastal origin as a result of early cessation of growth.

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Photosynthetic and Respiratory Rates In Leaves of Male and Female Quaking Aspens

BY
PHILIPPE F. BOURDEAU

DIFFERENCES IN VEGETATIVE development related to sex have been reported for several dioecious tree species. Syrach Larsen (1937) stated that male specimens of *Juniperus communis* L. were taller and more slender than female trees. He also quoted several reports dealing with such diverse species as *Ginkgo biloba*, *Taxus baccata*, *Fraxinus excelsior*, and *Populus nigra* L. var. *italica* Muenchh. In all cases the male plants were either more vigorous or had better form.

Working with American species of poplar, Pauley (1949) observed that of 76 clones selected on the basis of vigor, health, and stem form, only 18 (23.7 percent) were female. He pointed out, however, that in nature, the sex ratio is unbalanced toward maleness, which might partly explain the predominance of male clones in this selection. Pauley and Mennel (1957) reported that in a wild population of quaking aspens, *Populus tremuloides* Michx., males, or predominantly males, outnumbered females by a factor of three and that the incidence of hermaphroditism was considerably higher among females (20.6 percent) than among males (4 percent). If the mechanism of sex determination in poplar calls for a 1:1 ratio, the actual sex distribution might indicate greater survival ability in male plants.

Muhle Larsen (1954) examined several groups of hybrid aspen seedlings (*P. tremula* x *P. tremuloides*) and found that the average height of a group was positively correlated with the proportion of male individuals it contained.

Another kind of sexual difference was reported by Deleano and Dick (1937) who found that throughout the entire growing season, leaves of male *Salix gracilis* and *Populus alba* trees contained, on the average, more chlorophyll than leaves of female trees.

In trees that are flowering, vegetative growth may be reduced to a greater degree in the female than in the male individuals because appreciable amounts of assimilates are diverted to the production of flowers, seeds and fruits, although it could be argued that, in some species, at least, as much material is utilized in producing large numbers of male flowers as in the formation of female parts.

Moreover, differences in growth rate between male and female individuals some-

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The author is Assistant Professor, School of Forestry, Yale University, New Haven, Connecticut. He wishes to express his gratitude to Dr. W. B. Critchfield, Cabot Foundation, Harvard University, who provided the plant material used in this study as well as the data on flower production. Acknowledgment is due to Miss Miriam L. Laverick for assistance in collecting the data.

times appear before the onset of flowering (Muhle Larsen).[1] Thus, actual differences in vegetative growth related to sex probably occur in dioecious species. Such differences might, conceivably, be related to the photosynthetic efficiency of the leaf. To explore this possibility the photosynthetic and respiratory rates of leaves of male and female quaking aspens were compared. The results obtained are presented here.

Materials and Methods

The aspen clones used came from a wild population in the vicinity of Petersham, Massachusetts. Root cuttings were collected in April, 1957, from 14 trees whose sex had been checked by flower sampling during the preceding year. All seven male individuals had borne male flowers only whereas most females had produced a few perfect flowers (Critchfield).[1] The root cuttings were planted in sandy loam and placed under glass. Vigorous shoots developed during the following two months. The potted plants were then left in a greenhouse until August 1957, when the measurements were made.

Photosynthetic and respiratory rates were determined under uniform conditions of temperature, light quality and intensity, and carbon dioxide concentration. Leaves were severed from the shoots and immediately placed horizontally in a low, cylindrical "Lucite" chamber, with the petiole bases enclosed in a small container of water. The chamber formed a closed system with an air pump and a Model 15-A Liston-Becker infrared CO_2 gas analyzer. Air was circulated at a constant rate of 3 liters per minute. Carbon dioxide concentration was maintained between 270 and 330 ppm. Carbon dioxide uptake or output by the leaf tissue was measured by the rate of concentration change in the system.

The light source was a Fluomeric[2] bulb, combining mercury arc and incandescent filaments. The light intensity reaching the upper surface of the leaf in the chamber (for the measurement of photosynthesis) was 2500 foot candles, or approximately 62,500 ergs/cm.^{2}/sec. of visible light. A temperature of 25° ± .5°C. was maintained, control being achieved by circulating cold water in the double roof of the chamber.

Measurements were made on fully-developed leaves from paired plants, one of either sex. After an induction period of at least 45 minutes at high light intensity, the photosynthetic activity was determined in successive runs of a few minutes each until a steady rate was attained. The chamber was then darkened to measure the respiration rate by the carbon dioxide output in darkness. Data were obtained in this manner on 12 male-female plant pairs.

After photosynthesis and respiration were measured, representative leaf samples were taken to determine the water content by oven-drying, the nitrogen content by the Kjeldahl method (A.O.A.C., 1955), and the chlorophyll content by spectrophotometry (MacKinney, 1941).

Results

The average values for photosynthesis, respiration and other leaf characteristics are presented in Table 1. The t-tests were carried out on the paired data in order to eliminate any variation due to differences in preconditioning the plants.

The average rate of net photosynthesis at 2500 foot candles in the female clones, per gram fresh leaf, was 10 percent less than that in the males, but this difference was not statistically significant because of the variability observed in photosynthetic rates. The average respiratory rate at 25°C., on the contrary, was 37 percent higher in leaves of female plants than in those of males, a difference significant at the 5 percent level. No significant correlation was found between the rates of photosynthesis and respiration in individual leaves of either sex. The rate of total photosynthesis (net photosynthesis plus respira-

[1]Personal communication.

[2]Manufactured by Duro-Test Corporation.

TABLE I. Average characteristics of leaves of male and female aspen clones. Photosynthesis at 2500 foot candles, 25°C. and 270-330 ppm CO_2. Respiration as CO_2 output in darkness at 25°C.

	Net photosynthesis, μg. CO_2/min./g. fresh leaf	Respiration, μg. CO_2/min./g. fresh leaf	Total photo-synthesis μg. CO_2 min./g. fresh leaf	Leaf area, $cm.^2$	Leaf weight, mg. (fresh basis)	Leaf weight, mg. (dry basis)	Leaf weight, mg. /cm^2 (fresh basis)	Leaf nitrogen, % (dry basis)	Leaf chlorophyll mg./g. (fresh basis)
Male	121.8	15.9	137.7	64.41	915	302	14.2	2.57	2.63
Female	109.1	21.8	130.9	60.27	899	300	15.1	2.50	2.27
Difference (♂ − ♀)	12.7	− 5.9[1]	6.8	4.14	16.0	2	− .9	.07	.36
Difference (% ♂ value)	10.4	−37.1	4.9	6.4	1.7	.7	− 6.3	2.7	13.7

[1]Significant at 5% level.

tion) was only 5 percent higher in leaves of male plants, a non-significant difference.

Similarly, the differences in surface area, water content, weight per unit area, and nitrogen content, observed between leaves of male and female plants, were small and non-significant. The chlorophyll content was 13.7 percent higher in the males, but the difference was not statistically significant.

The higher respiratory rates at 25°C. in leaves of female plants were not related to their nitrogen content. They might be due to a higher level of metabolic activity of the cells. If the differences in respiration of the magnitude observed here were to prevail throughout its life span, they would substantially reduce the photosynthetic efficiency of the leaf in females as compared to males. In this connection, it might be of interest to note the difference in mean radial increment between stems of the male and female ortets used in this study. For the same average age (12 years), mean ring width, as determined on increment cores collected at one foot above ground, was 3.9 mm. in the males and 2.9 mm. in the females. However, before drawing any general conclusions on the relationships between leaf photosynthetic efficiency, growth, and sex, it would be necessary to obtain more data on a large number of male and female clones, and to consider other attributes, such as total foliage area, seasonal changes in leaf activity, effective leaf life-span, and flower and seed production.

Summary

Determinations of photosynthetic and respiratory rates were made under standard conditions on paired leaf samples of male and female clones of quaking aspen.

Respiration rates were significantly higher in the leaves of female plants (37 percent more than in the males). Net photosynthesis and chlorophyll content were slightly, but not significantly, lower (10 and 14 percent, respectively) in the females.

Surface area, water content, weight per unit area, and nitrogen content were very similar in the leaves of both sexes.

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World Forest Products Statistics—A Ten-Year Summary, 1946-1955

By the Food and Agriculture Organization of the United Nations, Rome, February 1958. $3.00.

Steady expansion in the output of timber from the world's forests in the period 1946-1955 is pointed out in a 10-year summary of the world's statistics of forest products compiled by F.A.O. in collaboration with E.C.E.. Except for a slight decline between the years 1951 and 1953, the total harvest increased. Included are figures on timber removals, production of forest products and world trade with more than 150 countries and territories.

The world output of fuelwood is reported to have declined in relative importance, but the proportion of industrial wood increased. Coniferous species provided more than three-fourths of the industiral wood supply. Sawlogs, veneer logs, and logs for sleepers comprised the largest category of industrial wood. Among processed products, sawnwood remained the most important. Although North America produced the largest volume of sawnwood throughout the decade, the region reporting the most rapid rate of growth was the U.S.S.R.

Plywood had a phenomenal expansion. The leading plywood-producing countries in 1955 were the United States, the Soviet Union, Canada, Japan and the Federal Republic of Germany. The most rapid 10-year growth in output was reported from Asia (mostly Japan), followed by Central America (Mexico). The largest plywood exporter throughout the decade was Finland. The growth in export volume was especially noteworthy in Japan.

The woodpulp industry was dominated by North America and the three northern European countries: Finland, Norway and Sweden. During the decade Europe changed from a net exporter of woodpulp to a net importer, whereas North America showed the opposite development.

In newsprint production, North America and Europe continued to lead all other regions, but the rate of development in the Pacific Area and in Asia was outstanding. Canada was the leading newsprint-exporting country. The region producing the largest volume of paper other than newsprint was North America. The most rapid growth in production, however, was reported from Asia and the U.S.S.R. About 91 percent of the 1955 production of paperboard came from North America and Europe. Fibreboard had been produced mostly in North America and Europe, but substantial increases in output were reported from the U.S.S.R and the Pacific Area. The volume of production in 1955 was highest in the United States.

The publication contains 51 tables, 12 charts and text in three languages: English, French and Spanish.

The Effect of Defoliation on Foliage Production and Radial Growth of Quaking Aspen

BY
A. H. ROSE

DURING THE COURSE of phenological studies of forest insects and their food plants in the Sioux Lookout District of Ontario during the period 1950 to 1953, an opportunity was afforded of obtaining comparative records of development of the forest tent caterpillar (*Malacosoma disstria* Hbn.) and its favored food plant quaking aspen (*Populus tremuloides* Michx.) and of assessing the effect on the tree of defoliation by this insect. In the early spring of 1953 frost, sleet, and hail killed the developing aspen foliage (hereafter referred to as weather defoliation) and brought about the destruction of the tent caterpillar population (Blais *et al.*, 1955). This made it possible to determine the effect on the tree of a second type of defoliation.

Aspen growth and tent caterpillar development were observed in a series of study plots of differing tent caterpillar infestation history and intensity. Records were made of the time of occurrence of a number of features of aspen growth through periodic examination of buds and foliage, and of tent caterpillar development by sampling larval and pupal populations. The date when half the sample reached or passed each specified stage was selected, for comparative purposes, as the time of occurrence of each stage. Records of defoliation and development of aspen, and of general tent caterpillar activity were also maintained. Seasonal radial growth of aspen (at breast height) was measured periodically with a dendrometer (Belyea *et al.*, 1951), and shoot growth by means of calipers and ruler.

Defoliation in study plots was recorded according to the following classes:

Complete: loss of the entire leaf-blade surface of the tree and the destruction of the apex of vigorous shoots.

Severe: loss of most of the leaf-blade surface; many partially eaten leaves in the upper crown, and many intact leaves on smaller branches in the lower crown.

Medium: loss of many leaves; many partially eaten leaves in the upper crown, most leaves in the lower crown intact.

Light: loss of some leaves from some of the larger branches in the upper crown, lower crown intact.

These categories differ somewhat from those of Hodson (1941) who recognized only heavy, medium, and light. Hodson's "heavy" category probably included both

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"complete" and "severe" as defined above, the other two being roughly similar. It is essential here to differentiate between complete and severe because of differences noted in the response of the tree to these two degrees of defoliation.

Seasonal Development in Aspen and in the Tent Caterpillar

Table 1 lists, in sequence, the dates of occurrence, during the four study years, of a number of features of tent caterpillar and aspen development, and clearly demonstrates their synchronization, particularly in the early part of the season. Most striking is the coincidence of egg hatch and bud opening, also recorded by Hodson (1941), which ensures a readily accessible food supply for newly-hatched larvae.

During the first three instars the larvae are gregarious and feeding was restricted to the shoots arising from the twigs on which the eggs had been laid. Both leaf number and size increased and shoots began to elongate during this period (Fig. 1). Radial growth began about a week after bud opening and larval emergence, and soon reached a high rate (Table 1, Fig. 2). In the fourth instar the larvae become solitary feeders and feeding occurs throughout the crown. During the last two instars they wander (Hodson, 1941, Sullivan and Wellington, 1953) and are found on most plants in the area, especially the shrubs.

The last larval instar of the tent caterpillar occurred when at least one-fourth of the radial growth had been put on by normal aspen trees (Table 1, Fig. 2). At this time basal aspen leaves were fully grown and some lateral buds on the new shoot were readily visible, and leaf production and linear growth of vigorous shoots were at least one-half completed (Table 1, Fig. 1). By the time larval feeding was essentially completed, about one-half of the annual radial growth had been laid down, and linear growth and leaf production were still two to three weeks from completion in normal trees (Figs. 1 and 2). Thus larval

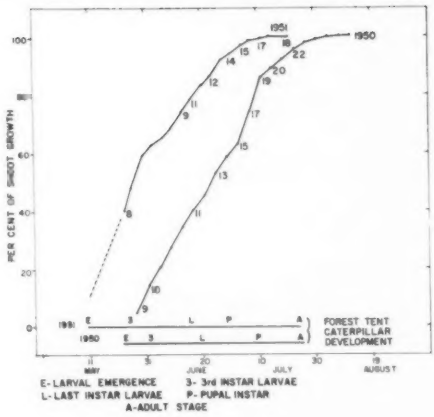

FIGURE 1. *Cumulative growth in a typical vigorous shoot of quaking aspen in 1950 and 1951 and forest tent caterpillar development. Numerals below each curve indicate number of unfurled leaves present on the shoot at different times.*

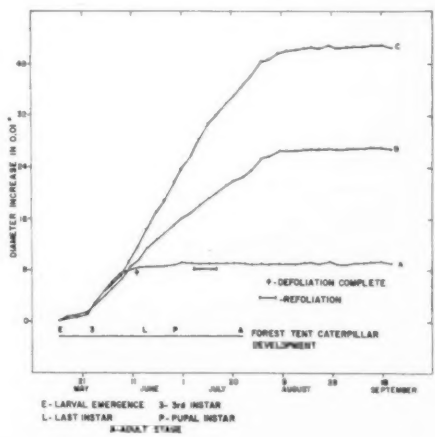

FIGURE 2. *Cumulative radial growth (shown as diameter increase) in three quaking aspen trees with differing degrees of defoliation from one stand in 1951, and forest tent caterpillar development. A. Completely defoliated. B. Partially defoliated. C. Not defoliated.*

feeding, and consequently foliage destruction, ceased well in advance of normal completion of both radial and linear growth and foliage production.

During early larval feeding, foliage was produced more rapidly than it was consumed; as a result some shoot and radial growth always occurred, even in trees ultimately completely defoliated. During the last larval instar, however, foliage destruction was very rapid, and trees appeared to be stripped of their foliage overnight, a fact readily appreciated since Hodson (1941) has shown that 80 percent of the total food requirement of the tent caterpillar is consumed during the last instar.

Defoliation of aspen trees in the spring of 1953, as a result of adverse weather conditions, was generally severe. Blais *et al.* (1955) have given an account of weather conditions that existed and their effect on both aspen foliage and tent caterpillar populations throughout an extensive area in Ontario west of Lake Superior. Briefly, abnormally high temperatures during the first nine days of May caused the hatching of tent caterpillar eggs and the opening of aspen buds. By May 10 basal leaves on the

TABLE 1. A chronology of development of forest tent caterpillar and of quaking aspen for four years.

Quaking aspen					Forest tent caterpillar				
Developmental feature	Date of occurrence[1] 1950	1951	1952	1953	Developmental feature	Date of occurrence[1] 1950	1951	1952	1953
Catkin fall	21/V	7/V	....	7/V	Larval emergence	23/V	9/V	1/V	8/V
Vegetative buds open	24/V	11/V	3/V	8/V					
Basal leaves unfurled	28/V	16/V	8/V	9/V					
Beginning radial growth	31/V	15/V	9/V	...[2]	3rd larval instar	1/VI	25/V	13/V	...[2]
Basal leaf full grown	16/VI	7/VI	31/V	....					
Quarter radial growth	21/VI	9/VI	7/VI	....	Last larval instar	19/VI	15/VI	10/VI	....
Half radial growth	7/VII	21/VI	14/VI	....	Prepupae	7/VII	26/VI	20/VI	....
					Pupae	9/VII	29/VI	24/VI	....
					Adults	25/VII	24/VII	5/VII	....
Shoot growth completed	12/VIII	21/VII	6/VII	....					
Radial growth completed	31/VIII	21/VIII	31/VII	....					

[1]Date when half or more of the sample exhibited the developmental feature.
[2]Partial information only available for 1953 because of the destruction of aspen foliage and tent caterpillar populations after May 10.

shoots had unfurled and egg hatching was virtually completed. During that day the temperature dropped steadily, and on the following morning reached 22° F.; this drop in temperature was accompanied by rain, sleet, and hail. For the next ten days low temperatures prevailed. Developing aspen foliage generally was killed, and although many young tent caterpillar larvae survived the cold, they soon starved for want of food, since the trees remained leafless for about five weeks. In the area affected tent caterpillar populations virtually disappeared, and damage to developing aspen shoots was severe.

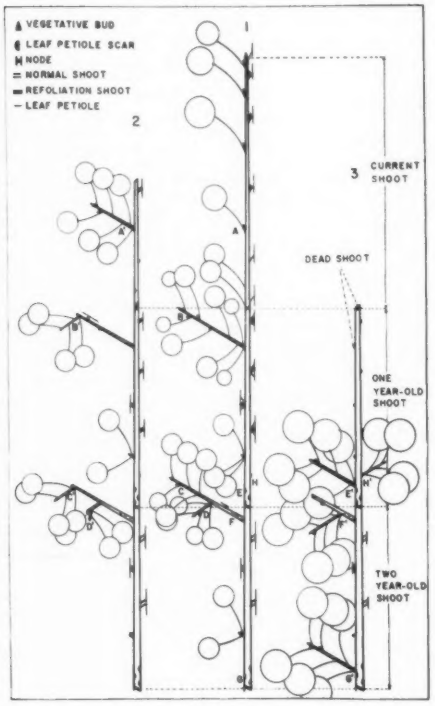

FIGURE 3. *A diagram of three years' growth in a quaking aspen branch at the end of the growing season. 1. Normal growth; A, B, C, and D indicate buds produced during the current season; E, F, and G indicate leaf petiole scars; H indicates a dormant bud. 2. The same branch if it had suffered complete tent caterpillar defoliation during the current season and had refoliated; A', B', C', and D' indicate refoliation shoots produced from buds A - D in 1. 3. The same branch if it had suffered weather defoliation during the current season (of the type experienced in 1953) and had refoliated; E', F', and G' indicate refoliation shoots arising from the bud rudiments located above the leaf petiole scars E - G in 1; H' indicates a refoliation shoot arising from the dormant bud H in 1.*

Defoliation and Foliage Production

Although leaf production and tent caterpillar larval feeding commence at about the same time, leaf production continues for some two to three weeks after completion of larval feeding. In trees where larval feeding had been heavy but where growing tips had not been destroyed (severe defoliation), foliation continued following cessation of larval feeding. This often gave the general appearance of refoliation, or the production of a second set of leaves.

In trees that had lost their entire leaf complement and in which the majority of growing shoots had been destroyed (complete defoliation), continuation of leaf production was not possible; in these trees true refoliation occurred. Three to four weeks after defoliation was complete, buds in the axils of new leaf petioles, and terminal buds on dwarf shoots that would normally have remained dormant until the following year, opened and a new set of leaves was produced (Fig. 3). These leaves were about the same size as normal leaves, and because of their origin were primarily on the periphery of the crown.

In trees in which virtually all leaves and growing shoots had been killed by adverse weather in the spring of 1953, refoliation also occurred, but in this case it was mainly from development of bud rudiments located immediately above old leaf scars on 2- to 6-year-old twigs (Fig. 3). Some small dormant buds also produced shoots. Shoot growth from bud rudiments and dormant buds began about five weeks after the

earlier normal bud opening, and large leaves, similar to those of sucker growth, were produced. Because of their origin, these leaves were produced more in the centre of the crown, and many of the 1952 shoots at the periphery died back by autumn. Once again, refoliation only occurred after complete defoliation. Some trees were hit less severely by the freezing temperatures, and in these only the basal leaves were destroyed and the growing tips survived to produce a partial filling out of the crown through normal foliation. Such shoots ultimately bore a number of leaves near the apex and were bare near the base.

Aspen stands under close observation during the four study years, although geographically close together, exhibited varying degrees of tent caterpillar defoliation during 1950, 1951, and 1952, and of weather defoliation in 1953. Table 2 shows the defoliation history for three stands, one of which is divided into three portions, with information on the occurrence of true refoliation. In no stand was complete defoliation by the tent caterpillar experienced for more than one year, and true refoliation only occurred in that particular year. In 1953, true refoliation occurred only in those stands in which practically all new shoots were killed by adverse weather.

Defoliation and Radial Growth

Radial growth, according to Büsgen *et al.* (1929), is dependent on the newly formed assimilates of the leaves; therefore, loss of foliage should be reflected in reduced radial growth. Radial growth of aspen began about one week after bud opening and tent caterpillar hatching (Table 1). Since the amount of foliage consumed by young larvae is small, and since foliage production until the time of the last-instar larvae proceeded more rapidly than its destruction,

TABLE 2. A history of defoliation and refoliation caused by tent caterpillar feeding and severe weather in three aspen stands.

		Cause and severity of defoliation by years			
		Tent caterpillar			Weather
		1950	1951	1952	1953
	Stand A:				
(1)	Defoliation	Complete	Severe	Severe	Complete
	Refoliation	Yes	No	No	Yes
(2)	Defoliation	Negligible	Complete	Medium to severe	Complete
	Refoliation	No	Yes	No	Yes
(3)	Defoliation	Negligible	Light	Complete	Complete
	Refoliation	No	No	Yes	Yes
	Stand B:				
	Defoliation	Negligible	Severe to complete	Light to medium	Medium
	Refoliation	No	Yes[1]	No	No
	Stand C:				
	Defoliation	None	None	Medium to complete	Severe
	Refoliation	No	No	Yes[1]	Yes

[1]Only in completely defoliated trees.

radial growth was not initially affected. Thus in all trees, regardless of the severity of defoliation they ultimately suffered, three to four weeks' radial growth was laid down before the last larval stage was reached and heavy feeding occurred. This is markedly illustrated in Figure 2. The resulting reduction in radial growth depended on the severity of ultimate defoliation. In completely defoliated trees radial growth ceased at the time defoliation was complete, and did not resume that year even if the trees refoliated (Fig. 2, Curve A; Fig. 4A). Lesser degrees of defoliation resulted in a reduction in radial growth and an earlier than normal cessation of growth for the year (Fig. 2, Curve B; Fig. 4C). Recovery from severe radial growth suppression caused by tent caterpillar defoliation was often marked in the following year even when partial defoliation occurred (Fig. 4B).

Weather defoliation in 1953 also produced a severe suppression in radial growth. Since foliage was killed before radial growth started, the beginning of radial growth was delayed until new leaves had been formed by undamaged shoot tips in less severely damaged trees, or from bud rudiments or dormant buds in severely damaged trees. Ultimate radial growth for 1953 was greater in the former trees (Fig. 4B, C) than in the latter (Fig. 4A). Two years later (1955) radial growth had recovered to its pre-defoliation level (Fig. 4).

Twig and Tree Mortality

Batzer *et al.* (1954) and Batzer (1955) report an increase in crown dieback with increased frequency of defoliation by the tent caterpillar. Dieback of twigs and shoots observed soon after complete defoliation by the tent caterpillar amounted to those parts of the current year's shoots above the most apical refoliation shoot (all above A′ Branch 2, Fig. 3). When de-

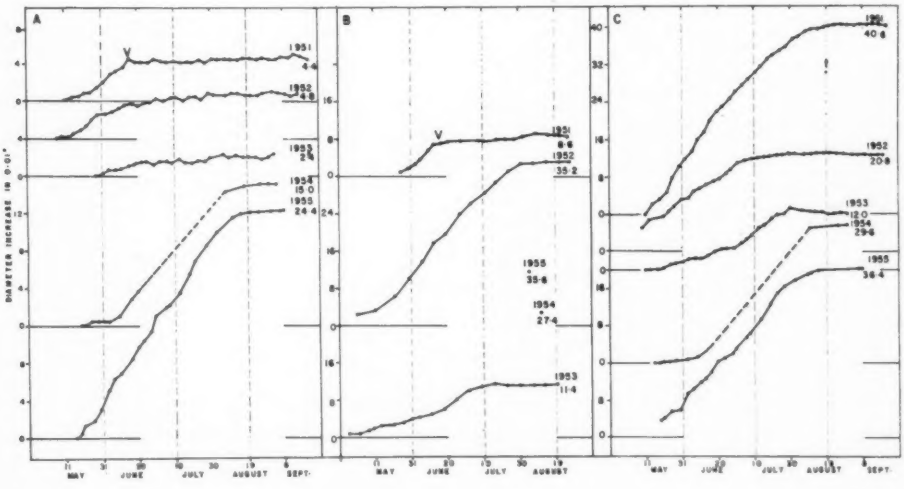

FIGURE 4. *Radial growth shown as diameter increase in typical trees from three aspen stands. A. Tent caterpillar defoliation complete in 1951, severe in 1952; weather defoliation complete in 1953. B. Tent caterpillar defoliation severe in 1951, light in 1952; weather defoliation medium in 1953. C. Tent caterpillar defoliation medium in 1952; weather defoliation severe in 1953. (V indicates date by which defoliation was complete.)*

foliation was caused by adverse weather the current year's shoot growth was lost and those parts of the previous year's shoots above the most apical refoliation shoot (all above H′ Branch 3, Fig. 3) died back. Thus, loss of almost two years of elongation resulted from the latter type of defoliation. No counts of twig mortality were made during the present study but considerable aspen twig and branch mortality was evident in 1954. It is probable that, because of the severity of damage to the shoots caused by adverse weather, much of the mortality observed in 1954 can be attributed to that cause.

Tree mortality following tent caterpillar and weather defoliation was negligible. Only one low-vigor tree in each stand died in the late summer of 1953, suggesting that weather defoliation was the primary cause and that tent caterpillar defoliation was, at most, a contributing factor. This substantiates reports of Batzer *et al.* (1954) and Batzer (1955) that tent caterpillar feeding did not cause tree mortality; Barter and Cameron (1955) had the same opinion but suggested that borers and bark beetles were largely responsible for tree mortality.

Discussion

Hodson (1941) reported that in Minnesota most aspen leaves had attained full size by the time tent caterpillar larvae reached the second last instar—or, that aspen foliage was fully developed by the time defoliation was completed. Similarly, Barter and Cameron (1955) reported that in New Brunswick in two out of three years defoliation was not completed until aspen foliage was fully developed, and in the third year until it was half developed. In northwestern Ontario defoliation was invariably completed before normal cessation of shoot and leaf growth, thus accounting for the continuation of foliation (apparent refoliation) of trees stripped of leaves but in which the tips of growing shoots had not been destroyed. During the present study true refoliation only occurred after complete defoliation accompanied by the destruction of developing shoot tips and the new leaves were produced from buds that normally would not have developed until the following year. Complete defoliation of the same type did not occur in successive years.

Cessation of radial growth following defoliation, and resumption following later refoliation, are reported by Dils and Day (1950) in Michigan, and by Barter and Cameron (1955) in New Brunswick. In the present study, no cessation of radial growth was recorded after any degree of defoliation less than complete, but rather a slowing down of growth throughout the remainder of the normal growing period, resulting in a reduction in total yearly growth (Figs. 2 and 4C). In completely defoliated trees, growth ceased on completion of defoliation and did not resume for the balance of the season, even though true refoliation took place.

European workers (Büsgen *et al.*, 1929) attributed the production of double rings in one year to the production of two sets of leaves. Glock (1955) referred to a number of workers in North America who attributed double ring formation in one year to defoliation, and to others from more northerly localities who did not feel that two rings were formed in one year. He suggested that latitude may be a factor in the tendency to double ring formation. Two types of defoliation occurred during this study, one by tent caterpillar feeding when about one-fourth of the radial growth had been laid down, the other by adverse weather before growth had begun. Neither type of defoliation resulted in the formation of a double growth ring in the lower trunk of quaking aspen.

Büsgen *et al.* (1929) and Glock (1955) also attributed missing growth rings to the effects of defoliation. In the present study some radial growth was laid down before defoliation by the tent caterpillar occurred, but when weather defoliation occurred before growth began, growth occurred after

releafing. No evidence was found of completely missing rings in the lower trunk of quaking aspen defoliated either by the tent caterpillar or by adverse weather.

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Growth and Climate in Relation to Dieback of Yellow Birch

BY
J. CLARK
G. W. BARTER

BIRCH DECADENCE has been widely observed in North America and reported by many authors over the past 60 years (Balch and Prebble, 1940). It is associated with a variety of causal factors, operating singly or in combination, such as exposure through cutting of other species, insect defoliation, overmaturity or attack by the bronze birch borer (*Agrilus anxius* Gory). Spaulding and MacAloney (1931) and Hall (1933) noted that paper (white) birch (*Betula papyrifera* Marsh.) was more susceptible to decadence than yellow birch (*B. alleghaniensis* Britton) and described the symptoms as follows: thinness, curling, and eventual loss of the foliage in the topmost twigs, followed by dying back of the smaller then the larger branches with a tendency to retain normal foliage at the bases of the larger branches.

The deterioration of birch which began in central New Brunswick in 1932 reached such staggering proportions in a few years that it was recognized as a much more serious condition than decadence (Balch and Prebble, 1940). Its symptoms, in many respects similar to those of decadence, are briefly as follows: small chlorotic leaves or shrivelling of foliage often general throughout the crown, failure of buds, dying back of twigs and branches, followed in most cases by death of the tree in three to six years. A more specific and detailed description of the symptoms is given by Berbee (1957). Two important differences between this type of deterioration and the previously reported decadence are that it has affected undisturbed stands of all ages and that yellow birch appears more susceptible than paper birch (Balch and Prebble, 1940). The condition has come to be known as "dieback" although it is not always easily differentiated from decadence by casual observation.

The bronze birch borer, itself capable of injuring and killing healthy trees (Barter, 1957), is usually associated with dieback but it is not the initiating factor (Balch and Prebble, 1940; Nash, 1943; Pomerleau, 1944; Lambert, 1944; Hawboldt and Skolko, 1948; Quirke, 1953). Attempts to isolate a fungus that might have initiated dieback in the crowns of trees were unsuc-

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The authors are Research Officers at the Forest Biology Laboratory, Fredericton, N. B. Contribution No. 477, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada. Based in part on a thesis by J. Clark presented in June, 1952 to the Faculty of Graduate Studies and Research, McGill University, in partial fulfilment of the requirements for the degree of Master of Science. Acknowledgment is due to D. B. Carter, Research Associate, The Laboratory of Climatology, Centerton, N. J. for expert guidance with certain aspects of the water balance concept; to R. F. Morris for permission to use his unpublished growth data from the Green River area; and to R. E. Balch and M. L. Prebble for their constructive criticism of the original manuscript.

cessful (Hawboldt, 1952; Hansbrough, 1953; Redmond, 1955). Early investigations failed to produce evidence that a virus was involved (Hansbrough and Stout, 1947; Hansbrough *et al.*, 1950). Recently, however, virus-like symptoms associated with dieback have been transmitted from typical dieback trees to healthy seedlings and older yellow birch trees by grafting (Berbee, 1957).

Hawboldt and Greenidge (1952) reported that the first symptom of dieback was the dying of rootlets. Greenidge (1951, 1953) suggested that the moribund condition of the root system might prevent normal restocking of the tree's water content after its depletion by transpiration. He found that the water content of aerial portions of diseased trees decreased as dieback progressed, but could not find temporary or permanent stoppages in the water-conducting tissues. Clark and Gibbs (1957) showed that the seasonal moisture content of yellow birch twigs was disturbed from the normal pattern during drought years when soil moisture was deficient. Redmond (1955) increased yellow birch rootlet mortality by raising soil temperature which upset population balances of fungi inhabiting the roots and rhizosphere, and disturbed the development of mycorrhiza.

Martineau (1948) found a relationship between damage and stand density, age, and tree diameter. Nash *et al.* (1951) indicated that mortality was greater on dry, shallow soils. Greenidge (1949) found no relation between the occurrence of dieback and site condition, and suppressed trees were least affected. Balch and Prebble (1940) noted that affected trees covered a wide range of ages but that younger stands suffered less injury. Barter and Balch (1950) drew attention to the fact that the dieback symptoms appeared first in central New Brunswick and later in other parts of the Maritime Provinces, indicating an apparent spread of the disease. Daviault (1953) found a similar suggestion of spread in the Province of Quebec. On the other hand Pomerleau (1949) and Hawboldt (1952) do not believe that dieback has spread but merely varies in intensity from one locality to another. From observations made in 1956, Braathe (1958) suggests that dieback might have occurred simultaneously throughout the affected region and attempts to relate its beginning to the March thaw of 1936.

During studies on the role of the bronze birch borer in dieback Barter (1953, 1957) collected data on the radial growth, crown condition, and mortality of birch and associated hardwoods in eastern Canada, mainly the Maritime Provinces. Climatic analyses were carried out by Clark in connection with a study of the physiology of yellow birch and particularly the water requirements of that species (Clark and Gibbs, 1957). This paper brings together those results of these separate studies that provide evidence regarding the spread of birch dieback and the relation of the disease to measurable climatic factors.

Studies of Radial Growth and Mortality

Method. Before the controversial question regarding the spread of dieback could be answered fairly, it was necessary to find an impersonal, unbiased and consistent means of dating the occurrence of the disease. As a means to this end, the growth of yellow birch was compared with that of a non-susceptible species, sugar maple (*Acer saccharum* Marsh.) over a period beginning 15 years before the earliest reported appearance of the disease, to discover any dissimilarity or discontinuity related to its onset. These studies were restricted to yellow birch and sugar maple for the following reasons. Firstly, sugar maple and yellow birch are truly associates; they generally grow in mixture, their ranges practically coincide (Harlow and Harrar, 1941; Anon., 1949), and their soil moisture regimes are similar (Fraser, 1957). Secondly, paper birch is not a satisfactory species for the study of normal growth trends be-

cause its growth pattern is confused by periodic outbreaks of defoliators (Fig. 1, A, B) and it is subject to considerable mortality through the cumulative effects of defoliation and bronze birch borer attacks (Barter and Cameron, 1955) when yellow birch stands in the same area suffer little or no damage. Similarly, widespread outbreaks of the birch leaf skeletonizer (*Bucculatrix canadensisella* (Chamb.) and birch sawfly (*Heterarthrus nemoratus* Fall.), in the late 1920's affected the crowns and growth of paper birch but caused little or no damage to yellow birch (Simpson, 1932). In addition, paper birch, less tolerant of shade and shorter-lived than yellow birch, occurs mostly in even-aged stands and is considerably affected by competition (Fig. 1, B, C). Spaulding and MacAloney stated "seedling paper birch matures at about 75 years . . ., at 50 years it has begun to decline in vigor and prob-

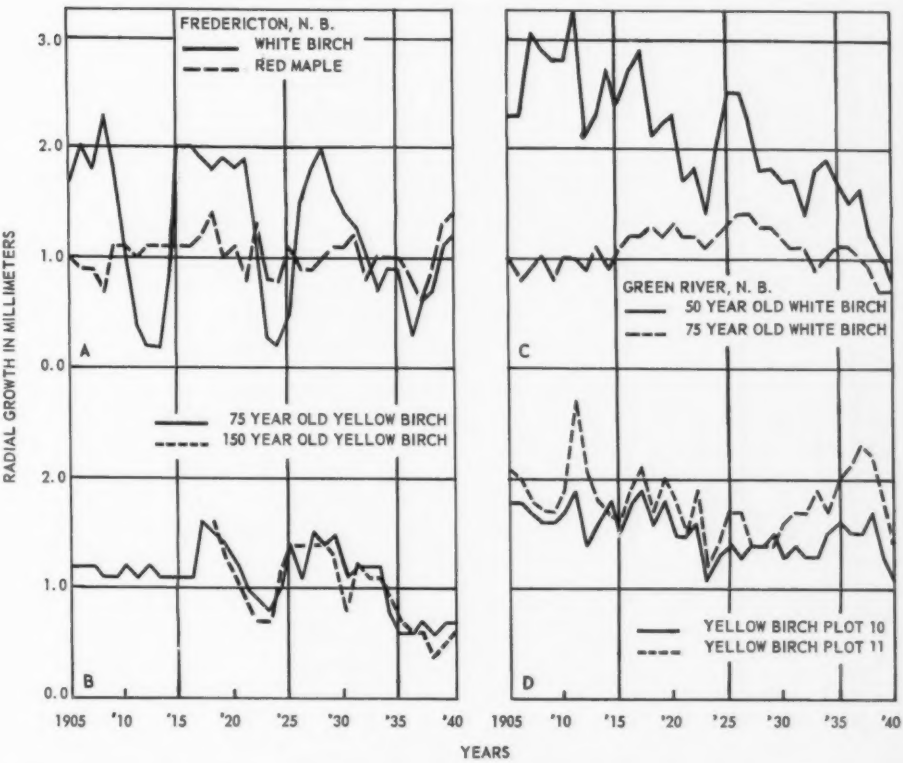

FIGURE 1. *Curves of radial growth. A. Paper birch growth reduced by three outbreaks of the forest tent caterpillar, effects of the third outbreak in 1933 and 1934 are combined with those of the early years of dieback. Red maple, as a check, is not attacked by the insect or the dieback. B. Similar growth trends in two yellow birch stands of different ages 1 mile apart. C. Dissimilar growth trends in two paper birch stands of different ages about 5 miles apart. D. Similar growth trends in two yellow birch stands of the same age 5 miles apart. (A, C, and D from unpublished data of R. F. Morris with his permission.)*

ably actual decadence from old age has begun although it may not be perceptible." All these possible causes of deterioration in paper birch increase the danger of confusing them, or disturbed growth patterns due to them, with the effects of climate or dieback. Reports concerning dieback based largely on crown condition and growth of this species are therefore suspect. Thirdly, in the Maritime Provinces the growth patterns of other hardwood associates of yellow birch have been affected by various factors which make them unreliable as a basis for this study: beech (*Fagus grandifolia* Ehrh.) by the beech scale (*Cryptococcus fagi* (Baer.)) and Nectria fungus; gray birch (*Betula populifolia* Marsh.) by various leaf miners and skeletonizers; and the poplars by the forest tent caterpillar (*Malacasoma disstria* Hbn.), bronze poplar borer (*Agrilus liragus* B. & B.), and hypoxylon canker (*Hypoxylon pruinatum*).

In all cases growth measurements were made on dominant or co-dominant trees.

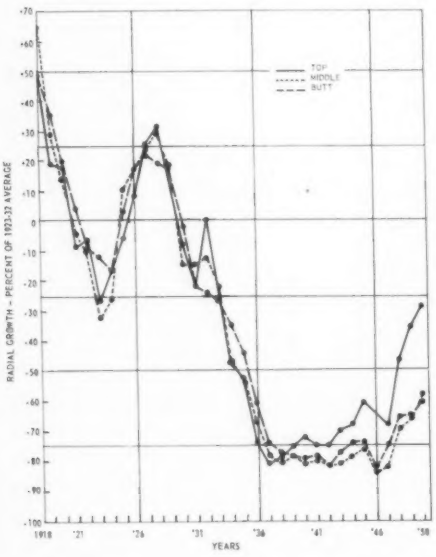

FIGURE 2. *Average radial growth of 10 surviving yellow birch trees near Fredericton, N. B.*

Radial growth of healthy maples was compared with that of yellow birch trees in classes 1 to 4B of the following tree classification system:

1. Normal.
2. Foliage thin, off-color particularly in upper crown, but no bare twigs or branches.

3A. Dead twigs but no dead branches. Such twigs occurring at the ends of the branches, usually in the top of the crown and for a distance of about 2 to 3 feet from the edge of the crown. In this and subsequent categories, the foliage is usually but not necessarily weak.

3B. Dead branches to the extent of one-half of the crown area.

4A. More than half of the crown dead.

4B. As in 4A, but no living branches except small adventitious ones, usually at the base of the crown or on the stem.

5A. Tree dead, but cambium green at B.H.

5B. As in 5A, but cambium dry at B.H. Most of the fine twigs still adhering.

6. Tree dead several years, most of the twigs and smaller branches gone.

To determine the distribution of growth accompanying dieback, detailed analyses of ten yellow birch trees were made by measuring the growth rings on four radii of polished cross-sections at each of three levels: butt (1 ft. above the felling cut), top (where the main stem was about 2 in. in diameter), and middle (midway between the first two). Growth curves so determined (Fig. 2) clearly show that reduction of growth occurred simultaneously throughout the tree. In addition, growth measurements of four cores per tree (one from each quadrant) at breast height were compared with two cores per tree (on the average diameter) at breast height and found to give similar growth trends. All further growth studies were made using two cores only from opposite sides at breast height. Increment cores were air-dried, smoothed with a small electric sander or scalpel, painted with an aqueous solution of bismarck brown (1.0 g. per 500 ml.) to improve the resolution of small rings, and measured to the nearest .01 mm. with a binocular microscope and ocular micrometer attachment.

The progressive crown deterioration accompanying dieback is reflected in the radial growth: the early symptoms usually by a brief period of erratic decline (occasionally by a marked decline suggesting systemic shock), advanced symptoms by a rapid growth reduction, and severe crown injury by a few years of very slow growth which ceases with the death of the tree. In residual trees showing signs of crown recovery, the third stage (very slow growth) is followed by an increasing growth rate which becomes apparent first high up in the trunk (Fig. 2).

Prior to dieback the growth patterns of birch and maple were similar, but as definite crown symptoms became obvious the growth of diseased birch fell off while that of maple continued to fluctuate normally. A few birch trees (up to 5 percent in some stands) never became severely affected by dieback. In these the growth pattern resembled that of sugar maple more than that of badly diseased yellow birch (Fig. 3). However, their numbers were unevenly distributed, completely absent in some stands, whereas maple was always found in association with the diseased birch. Therefore, the growth of maple is used here as a more reliable and consistent check. This readily measured divergence of birch and maple growth is used here to date the onset of dieback in preference to early crown symptoms which could be, and have been, confused with those of decadence from other causes. However, growth divergence does not "pinpoint" the earliest

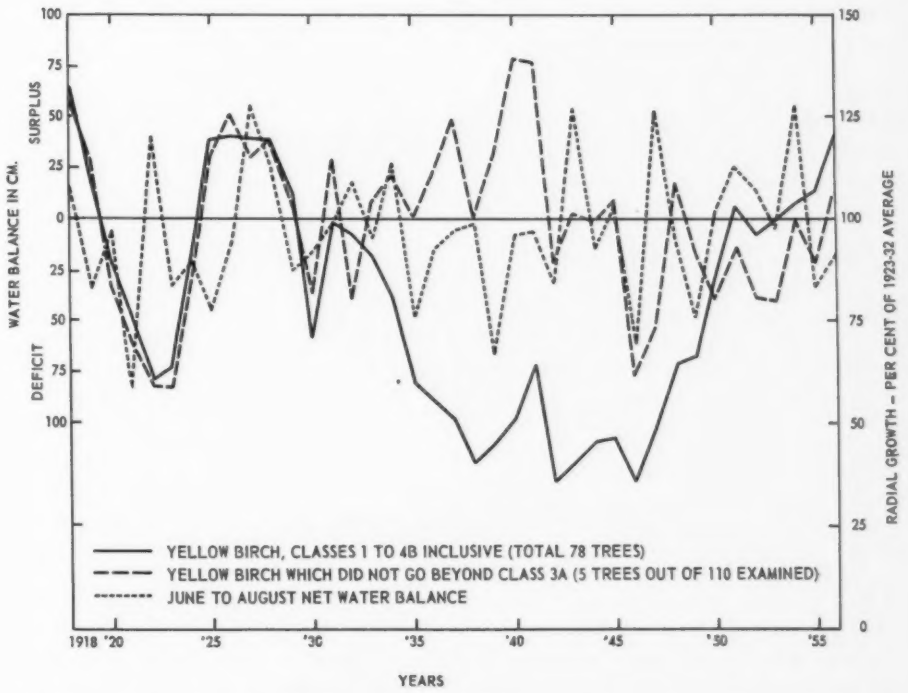

FIGURE 3. *Average radial growth of 78 diseased and 5 healthy or lightly injured yellow birch, and the June-August net water balance at Fredericton, N. B.*

symptoms. Permanent sample plot studies of crown injury and mortality, along with growth data, indicate that divergence occurs approximately three years after the first crown symptoms are noticeable. Death of individual trees commences in an area about the time that the general growth patterns show divergence or shortly thereafter. It is possible, therefore, to estimate fairly accurately the time of onset of dieback and the beginning of mortality by the growth divergence method.

Results. Over a long period of time the growth trends of birch and maple were similar, as one would expect of closely associated species responding to the same physical factors of environment. In four widely-separated areas (Fig. 4) the similarity was lost at the point of divergence where the growth of birch was reduced rapidly to an all-time low while that of maple continued to fluctuate about the mean or to increase.[1] We must therefore assume the introduction of some factor deleterious to birch but not to maple. The post-divergence increase in the maple growth at Fredericton is due largely to release following birch injury and mortality.

The points of divergence are distinct in all areas but in only two do they occur in the same year. Divergence occurred at Fredericton in1935, at Green River (near Edmundston) and north-central Nova Scotia in 1940, and at Cape Breton in 1945. It is notable that the areas affected in 1940 are respectively northwest and southeast of the suspected focal point of dieback in central New Brunswick (Fig. 5), and approximately equidistant from it; this, along with the later date of divergence in Cape Breton, suggests spread.

The mortality curves for Fredericton and Cape Breton (Fig. 4) are based on annual examination of tagged trees in permanent sample plots. Comparable data are not available for the other two areas. When two sample plots were established at Green River in 1939, all the 139 tagged yellow birch trees were alive, but on re-examination in the late summer of 1944, 40 percent were dead. Since the greatest annual mortality recorded on permanent sample plots was about 14 percent (Fredericton 1941), it is safe to assume that all the 40 percent mortality in the Green River plots did not occur in 1943 and 1944. An extensive cruise in 1939, in which over 800 trees were classified, indicated that only 1 percent of the yellow birch in the Green River region was dead at that time. Based on these cruise data and growth measurements the beginning of mortality on the Green River Plots is estimated at 1940. This is indicated in Figure 4 by a dotted line. From cruise data obtained in 1942 in two areas in north-central Nova Scotia it was determined that 5 percent of the yellow birch was dead, which, according to accumulated mortality on other plots, would place the onset of mortality in this part of Nova Scotia at about 1940 (Fig. 4, dotted line). Just as later growth reduction indicates onset of dieback, the commencement of birch mortality in the four areas suggests spread of severe damage.

Discussion. The dates of the occurrence of dieback, based on the growth divergence method and the dated observations (generally based on advanced crown symptoms) of other workers, in different localities is shown in Figure 5. These indicate that dieback appeared later as the distance of each locality from central New Brunswick increased. About 1935 it occurred in the Fredericton area of New Brunswick (Fig. 5 A). Nash (1943) reported that the disease occurred in eastern Maine in 1939 (Fig. 5, I, J). At the same time (Fig. 5 H) dieback occurred in the Matapedia Valley (Brown, 1941; Martineau, 1948; Daviault, 1953). This record is supported by growth measurements of yellow birch

[1]In this study the sample included: 78 birch and 17 maple at Fredericton, N. B.; 25 birch and 24 maple in north-central Nova Scotia; 165 birch and 42 maple at Cape Breton, N. S.; 14 birch and 8 maple at Green River, N. B.

in the Cascapedia Valley, Quebec (Fig. 5 E), and mortality data for 510 birch in that region which were under observation since 1935. In 1940 light to moderate damage occurred in western Nova Scotia (Hawboldt, 1947) which agrees with the dating of dieback by growth measurements in the same locality (Fig. 5 B, F). At the same time dieback reached the northwestern boundary of New Brunswick (Fig. 5 D). Nash *et al.* (1951) reported that severe damage occurred in the Kennebec Valley, Maine, in 1942, and as far west as New Hampshire (adjacent to Rangely, Maine) in 1944 (Fig. 5 K, L). Hawboldt (1947) reported that early symptoms were apparent in Pictou County, Nova Scotia, in 1944 (Fig. 5 G). Farther east on Cape Breton Island growth data clearly show the presence of dieback in 1945 (Fig. 5 C) and plot studies on the Island since that time indicate a northeasterly advance of the disease.

An extensive survey of yellow birch crown conditions, in parts of eastern Canada, was carried out in 1947 and 1948 (Barter, 1949). This survey started at Green River, N. B., proceeded northward

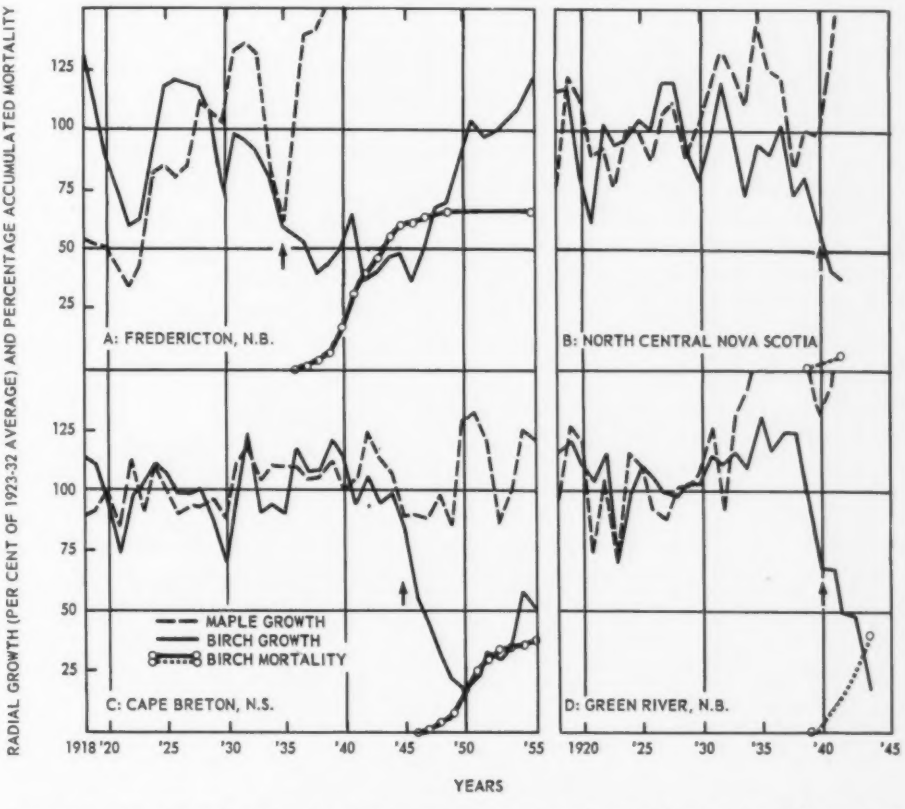

FIGURE 4. *Average radial growth and accumulated mortality of yellow birch and radial growth of sugar maple check trees for four widely separated areas in the Maritime Provinces. (D from unpublished data of R. F. Morris with his permission.) Growth divergence is indicated by arrow.*

into Quebec and westward from the Montmorency River watershed to the Lake Gagnon area north of Thurso; in Ontario it commenced at Chalk River and extended southward through Algonquin Park to Dorset, thence northward to North Bay and Timagami. Further observations were made westward from Sudbury to Sault Ste. Marie and northward about 125 miles along the Algoma Central Railway to Anjigomi.

At no place in Quebec was there evidence that dieback of yellow birch commenced as early as it did in New Brunswick. Westward from Quebec to the Algonquin Park region of Ontario, crown symptoms were progressively less severe and dieback more recent; farther west there was no visible evidence of dieback in yellow birch, either in crown symptoms or radial growth. It is interesting to note how the results of the above survey agree with a statement made by Daviault (1953) in a report on sample plot studies, in Quebec, from the Gaspé Peninsula westward to the Ottawa River during a 5-year period, 1947-1951: "The trouble which affects birch was first noted in the eastern part of the Province before it appeared in all the other regions in a westerly direction . . . this particular behavior of the disease is further substantiated by the fact that the damage it has caused to the present, becomes progressively less important as we proceed from east to west." Plot studies in Ontario (Sinclair, 1952) support these observations.

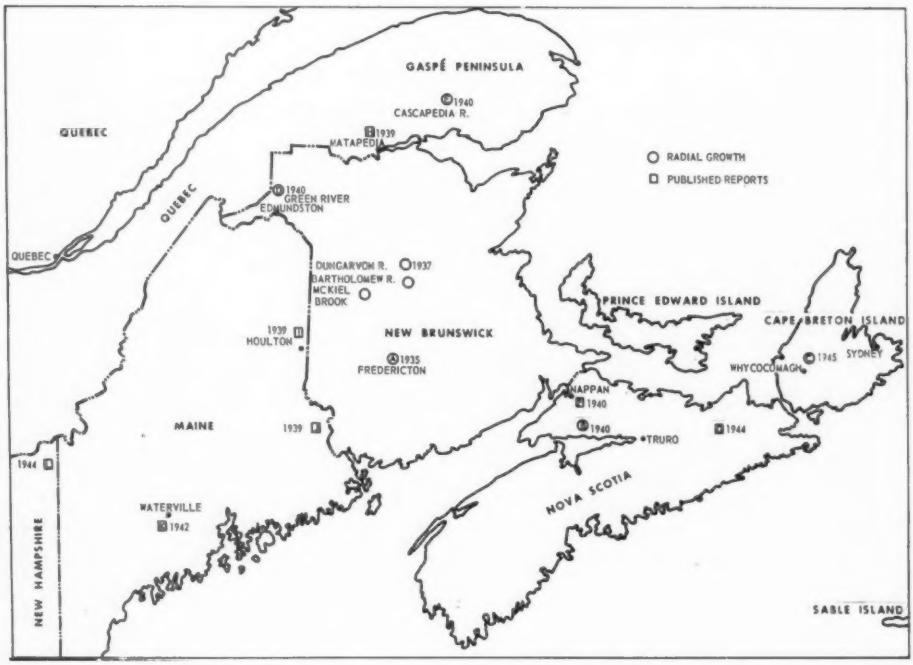

FIGURE 5. *The approximate dates of the occurrence of birch dieback in the Maritime Provinces of Canada and the northern New England States of U.S.A. as determined from studies of tree growth and published reports on the disease.*

Study of Climatic Factors

Several references may be found in the literature attributing dieback to climatic factors. There have been two main lines of thought: one stressing subnormal precipitation, the other above-normal temperature. In all cases, however, these factors have been dealt with separately. Such individual treatment is contrary to a basic principle in plant physiology, for it is well known that the moisture requirements of terrestrial plants increase with rising temperature. Therefore any scheme to correlate these climatic factors with plant growth should make provision for the effect of temperature on the water need of the plants; that is, on potential evapo-transpiration. Measurements of potential and actual evapo-transpiration can only be obtained from lysimeter studies but as these are scarce recourse must be made to the use of empirical formulae for calculating them. Thornthwaite (1948) and Thornthwaite and Mather (1955) devised formulae for calculating these important climatic factors from standard meteorological statistics as well as a simple bookkeeping procedure for determining the water balance. Though not perfected, the method is a valuable contribution to climatological and ecological research. Primarily designed to classify climatic regions, Thornthwaite's method is also useful for determining the seasonal, monthly, or daily water balance. For this reason climatic studies here[2] are based on Thornthwaite's concept of potential evapotranspiration which is more likely to expose periods of climatic stress that would not be obvious in the conventional sums of precipiation or averages of temperature.

In the water balance computations (Tables 1 and 2) the basic relations are: (1) potential evapo-transpiration (PE), estimated from temperature data, is regarded as the demand for moisture, and precipitation (P) as the moisture supply; (2) while P exceeds PE, the actual evapo-transpiration (AE) equals but cannot exceed the potential; there may be a surplus (S), provided soil moisture storage (ST) first reaches 300 mm., its assumed field capacity; and (3) while PE exceeds P, AE equals PE so long as moisture is available from the soil (Δ ST) to supplement P fully; afterward, AE is limited to concurrent precipitation and there is a deficit (D) equal to the difference between potential and actual evapo-transpiration.

It is apparent that the water balance is affected by temperature, total precipitation and distribution of precipitation. In eastern Canada the range of mean monthly temperature is not great, therefore monthly PE also has a rather restricted range and its influence on the water balance is not likely to be great. Figure 6 illustrates the range of monthly PE calculated from the recorded maximum and minimum mean monthly temperatures at four stations in the Maritime Provinces. By contrast, total monthly precipitation in eastern Canada is extremely variable from year to year and so has a great influence on the water balance. The maximum and minimum measurements of total monthly precipitation are also shown in Figure 6. Less obvious than total precipitation, but of equal or even greater importance, however, is the effect of distribution of precipitation on the seasonal *net* water balance (surplus minus deficit). Example computations (Table 2) for 1937 at Fredericton, N. B., illustrate this point: (1) the June to August net water balance calculated from actual meteorological data shows a deficiency of 7 mm.; (2) the interchange of June and August precipitation gives a net deficiency of 16 mm.; (3) the interchange of April and May precipitation results in a deficiency in the June to August net water balance of 28 mm. or

[2]The method used here follows exactly the procedure outlined in Appendix I, pp. 87-104, of "The Water Balance" by Thornthwaite and Mather, 1955, *op. cit.* which gives full instructions for evaluating the water balance, and the necessary tables and nomograms used to simplify the computations, along with worked examples.

four times that of the actual. The total precipitation is the same in all three examples. Variations in monthly precipitation as large as these theoretical values are possible as indicated by the curves of maximum and minimum recorded monthly precipitation for April to August at Fredericton (Fig. 6 A). Thus distribution of precipitation during or preceding the growing season has a very great influence on the net water balance of the growing season, but this is not taken into account in analyses based on total seasonal precipitation.

Results. The average length of the growing season of yellow birch was determined from weekly dendrometer measurements of radial growth at breast height for four years, 1948 to 1951, at Fredericton, N. B. On the average, 90 percent of the total growth takes place in the period June to August inclusive (Table 3); however, a

TABLE 1. Water balance by months computed from normals of mean temperature and precipitation for four stations in the Maritime Provinces of eastern Canada (all values in mm.).

Station and Years Obs.	J	F	M	A	M	J	J	A	S	O	N	D
Fredericton (67)												
Potential evapo-transpiration	0	0	0	44	71	106	128	112	72	38	2	0
Precipitation	98	79	91	75	79	96	89	101	90	104	97	87
Storage	300	300	300	300	300	290	254	245	263	300	300	300
Storage change	0	0	0	0	0	−10	−36	−9	+18	+37	0	0
Actual evapo-transpiration	0	0	0	44	71	106	125	110	72	38	2	0
Deficiency	0	0	0	0	0	0	3	2	0	0	0	0
Surplus	98	79	91	31	8	0	0	0	0	29	95	87
Sydney (69)												
P. E.	0	0	0	14	54	92	123	113	76	44	14	0
P	131	112	113	102	87	72	86	96	88	119	131	138
ST	300	300	300	300	300	280	248	234	246	300	300	300
Δ ST	0	0	0	0	0	−20	−32	−14	+12	+54	0	0
AE	0	0	0	14	54	92	118	110	76	44	14	0
D	0	0	0	0	0	0	5	3	0	0	0	0
S	131	112	113	88	33	0	0	0	0	21	117	138
Nappan (26)												
P. E.	0	0	0	21	66	100	123	110	73	42	7	0
P	84	70	98	67	58	77	69	81	81	101	91	99
ST	300	300	300	300	292	270	225	204	212	271	300	300
Δ ST	0	0	0	0	−8	−22	−45	−21	+8	+59	+29	0
AE	0	0	0	21	66	99	114	102	73	42	7	0
D	0	0	0	0	0	1	9	8	0	0	0	0
S	84	70	98	46	0	0	0	0	8	59	84	99
Edmundston (25)												
P. E.	0	0	0	18	68	108	124	107	69	32	0	0
P	74	55	45	51	76	98	105	85	88	72	77	63
ST	300	300	300	300	300	290	272	253	272	300	300	300
Δ ST	0	0	0	0	0	−10	−18	−19	+19	+28	0	0
AE	0	0	0	18	68	108	123	104	69	32	0	0
D	0	0	0	0	0	0	1	3	0	0	0	0
S	74	55	45	33	8	0	0	0	0	12	77	63

warm spring in 1949 noted elsewhere (Clark and Gibbs, 1957; Barter and Cameron, 1955) resulted in 15 percent of the seasonal growth occurring in May of that year. These measurements also showed a fairly good relationship between the rate of radial growth and weekly precipitation, indicating that yellow birch quickly responds to available moisture during active growth. May and September rainfall had practically no effect on the beginning and ending of seasonal growth.

Although the growing season of yellow birch, June through August, suggested that this might be the best period on which to base climatic analyses, it remained, however, to test other periods. Temperature, precipitation, and net water balance for periods of different lengths were compared with the growth of birch at four stations and tested by chi-square for significance. Three separate comparisons were made: (1) Trend, or the direction of change; if the climatic and annual growth data increased or decreased in the same year the relation was positive, whereas opposing changes were negative. In this comparison there was one degree of freedom. (2) Deviation; if the climatic data were above or below normal when the growth was respectively greater than or less than the average growth the relation was positive, where-

TABLE 3. A summary of seasonal radial growth of yellow birch from weekly dendrometer measurements during four years at Fredericton, N. B.

Year	No. trees	Percent of total growth		
		May	June to Aug.	Sept.
1948	3	7	88	5
1949	3	15	85	0
1950	38	8	91	1
1951	21	5	95	0

TABLE 2. The effect of distribution of precipitation on the June to August net water balance.

		Apr.	May	June	July	Aug.	Apr. to Aug. Totals	June to Aug. Net Bal.
Example 1								
Actual data	PE	24	79	110	[illegible]		480	
for Fredericton,	P	35	111	122		[illegible]	418	
N. B.	AE	24	79	110	[illegible]	119	461	
1937	D	0	0	0	[illegible]	12	19	7
	S	11	32	[illegible]	[illegible]	0	45	
Example 2								
As above but with	PE	24	79	110	136	131	480	
June and Aug.	P	35	111	82	68	122	418	
precipitation	AE	24	79	109	124	128	464	
interchanged	D	0	0	1	12	3	16	16
	S	11	32	0	0	0	43	
Example 3								
As in Example 1	PE	24	79	110	136	131	480	
but with Apr. and	P	111	35	122	68	82	418	
May precipitation	AE	24	76	110	125	114	449	
interchanged	D	0	3	0	11	17	31	28
	S	87	0	0	0	0	87	

as opposing deviations were negative. Again there was one degree of freedom. In both of these, complete randomization of the data should result in equal numbers of positive and negative relations, hence the "expected" values for the calculation of chi-square, with one degree of freedom, would be one-half of the total comparisons made in each case. (3) Trend and deviation combined; for a positive relationship both trend and deviation (as in 1 and 2 above) had to be positive at the same time; for a negative relationship both trend and deviation had to be negative at the same time. All other combinations of trend and deviation were given a rating of zero; i.e.,

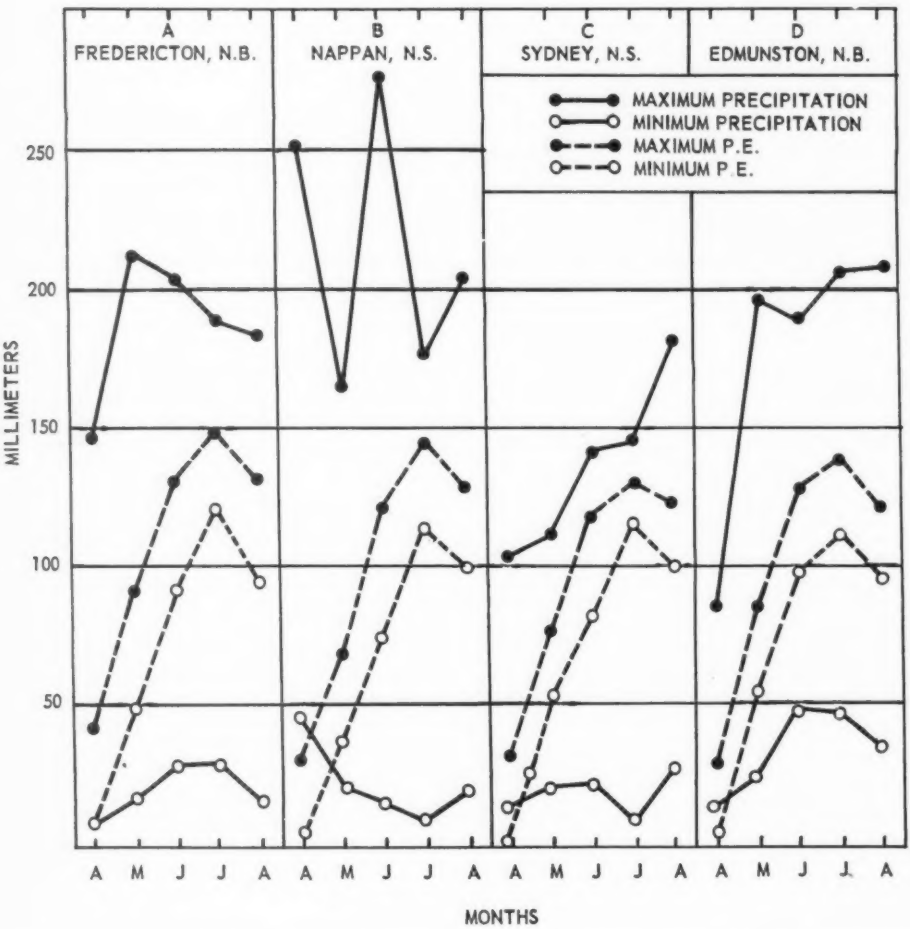

FIGURE 6. *Range of total monthly precipitation and range of monthly potential evapo-transpiration computed for maximum and minimum monthly mean temperatures, April to August inclusive, at the four stations and for the periods of years indicated in Table 1. Data from Meteorological Records, Department of Transport, Canada.*

no relationship. On this basis a random assortment of the data would result in the possible combinations illustrated in Figure 7; hence the expected values for the calculation of chi-square with 2 degrees of freedom would be in the ratio of 1:2:1. The results of these analyses are summarized in Table 4. It is necessary at this point to explain the terms "net water balance deviation from normal" and "net water balance." Calculated from the normal values of temperature and precipitation, the water balance at Fredericton, N. B., Edmundston, N. B., Nappan, N. S., and Sydney, N. S. (Table 1) shows small deficiencies occurring in the June to August period at all four stations. In other words the climate of the Maritime Provinces is characterized by a small summer deficiency and a large winter surplus. The annual water balance, derived from meteorological data for one year, generally deviates from the expected climatic balance. Discounting the expected (normal) deficiencies and surpluses from the annual water balance gives the "net water balance-deviation from

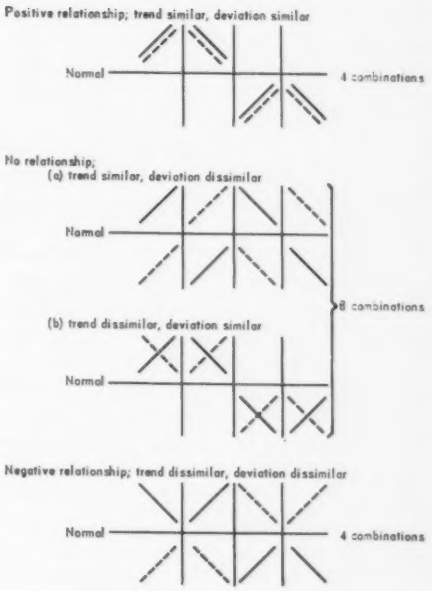

FIGURE 7. *Possible combinations in the index correlations of yellow birch radial growth and climatic factors.*

TABLE 4. Summary of statistical analyses of climatic factors and growth of yellow birch at four stations in the Maritime Provinces.

Analysis	Period	Significant chi-squares						
		Trend with 1 d.f.		Deviation with 1 d.f.		Trend and deviation with 2 d.f.		
		+	−	+	−	+	0	−
Precipitation, deviation from normal	Apr.–May	—	—	—	—	—	—	*
Precipitation, deviation from normal	June–Aug.	—	—	—	—	—	—	—
Precipitation, deviation from normal	Sept.–Oct.[1]	—	—	—	—	—	—	—
Temperature, deviation from normal	Apr.–May	—	—	—	—	—	—	—
Temperature, deviation from normal	June–Aug.	—	—	—	—	—	—	**
Temperature, deviation from normal	Sept.–Oct.[1]	—	—	—	—	—	—	—
Net water balance, deviation from normal	Apr.–Oct.	—	—	—	—	—	—	—
Net water balance, deviation from normal	June–July	—	—	—	—	*	—	—
Net water balance, deviation from normal	June–Aug.	—	—	—	—	*	—	—
Net water balance, deviation from normal (less Aug. surplus)	June–Aug.	—	—	—	—	*	—	—
Net water balance	Apr.–Oct.	—	—	—	**	—	—	—
Net water balance	June–July	—	—	—	—	*	—	—
Net water balance	June–Aug.	—	—	*	—	*	—	—
Net water balance (less Aug. surplus)	June–Aug.	—	—	—	—	—	—	—

[1]Compared with growth of following season.
**Significant at 1% level.
*Significant at 5% level.

normal." "Net water balance" does not discount the expected climatic (normal) surpluses and deficits but is simply the total surplus minus the total deficiency for the period indicated.

Based on trend alone climatic data showed no significant relationship with growth. For deviation alone the "June-August net water balance" gave a significant direct relationship, while the "April to October net water balance" gave a highly significant inverse relationship with growth. The extension of the net water balance period beyond that of the growing season reverses the relationship. When trend and deviation were tested together, 5 combinations of the net water balance for the period June-August gave significant positive results. On the other hand, precipitataion during April and May, and temperature during the three months of June-August gave a significant inverse relationship, with growth. The significant indirect relationship of the April-May precipitation, like that of the April-October water balance in the analysis of deviations above, again points out the disadvantage of extending the climatic period beyond the June to August growing season. The highly significant indirect relationship of the June-August temperature is synonymous, in effect, with a direct relationship by the June-August water balance inasmuch as the water balance is itself inversely related to temperature. Net water balance, especially during the growing season (June-August) or during the period when most of the growth takes place (June-July) is more closely related to radial growth than is precipitation. The June to August net water balance is the only combination that is significant in two out of three analyses. Thus the overall probability of wrongly accepting it becomes .05 x .05 or 1 in 400, which is less than the probabilities of similar errors associated with the acceptance of other combinations, even those that are highly significant in one column (Table 4).

In view of the sensitivity of yellow birch to available moisture during the period of active growth, it is not surprising to find that, in general, annual growth varies directly with the June to August net water balance (Fig. 8). The relationship is apparent both before the onset and during the course of dieback, indicating a continuous response of the trees to available moisture. However, the climatic data fail to explain the dramatic decline of annual growth to a minimum during the early years of dieback.

Except at Nappan, N. S. (Fig. 8 B), June to August net water balance deficiencies just before the onset and during the early years of dieback were less than those which had occurred in earlier periods. At Fredericton, N. B., water-deficient growing seasons had occurred from 1903 to 1909 and from 1923 to 1926 inclusive. Similarly at Sydney, N. S., successive deficiencies occurred from 1907 to 1914 and from 1928 to 1930 inclusive. There are no reports of widespread deterioration of yellow birch before 1918 that might be attributed to the earlier of these drought periods, nor is there evidence in the growth patterns since 1918 to indicate that the trees did not recover fully from the later drought periods. There is no evidence that abnormal climate preceded the onset of dieback in central New Brunswick about 1935 or in Cape Breton Island ten years later.

At Nappan, N. S., there were deficiencies in the June to August net water balance from 1932 to 1937 inclusive, but at Edmundston, N. B., for the same period deficiencies were negligible. Despite the more favorable water balance at the latter location, dieback (dated by sugar maple and yellow birch growth divergence) occurred simultaneously in north central Nova Scotia and northwestern New Brunswick. In addition, the pre-dieback rising growth trend and higher vigor of the Green River trees, contrasting with the declining growth trend and lower vigor of

those in central Nova Scotia, was neither a deterrent to the onset of dieback nor a guarantee against rapid growth reduction immediately thereafter. Indeed the more vigorous trees (Green River) suffered the greater growth-reduction. This observation is supported by growth data from vigorous and non-vigorous stands of yellow birch at McKiel Brook and Bartholomew River respectively, only 30 miles apart (Fig. 5). The similarity of their growth curves (Fig. 9) is no doubt due largely to the direct response of the two stands to the same climatic conditions but the simultaneous occurrence of dieback (about 1936 or 1937 by the growth divergence method of dating) caused a much more drastic growth reduction in the faster growing stand at McKiel Brook. Further investigation was made of vigor in relation to dieback by comparing the temporary growth reduction accompanying a known drought ot Fredericton, N. B., with the more prolonged reduction due to dieback (Fig. 10). It is evident that the more vigorous trees experienced the lesser growth decline during drought and the greater decline during the early years of dieback. Similar comparisons of data from other localities show that this behavior was fairly general throughout the Maritime Provinces. This does not mean, however, that the high vigor trees suffered the greatest mortality from dieback. The point is that vigorous and less vigorous stands and individual trees were affected simultaneously as dieback advanced into a locality, and that during the early years of dieback the more vigorous trees suffered the greater reduction in percentage of growth.

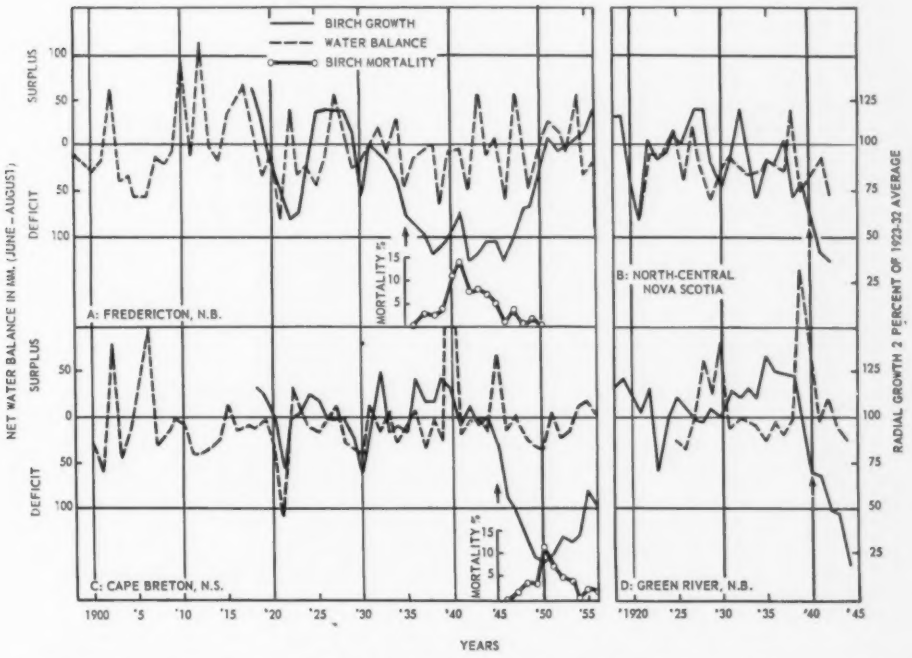

FIGURE 8. *Average radial growth and annual mortality of yellow birch and the June-August net water balance for the same localities represented in Figure 3.*

The post-dieback return to normal growth rate at Fredericton, N. B., and partial return to normal in Cape Breton Island, N. S. (Fig. 8 A, C), were not accompanied by outstanding changes in climate. The steady recovery at Fredericton continued despite a 3-year period of water deficiencies, 1948 to 1950 inclusive. Furthermore, with the exception of 1950, the June to August temperature at Fredericton was above normal from 1944 to 1953 inclusive. Similarly at Sydney, N. S., the June to August temperature was above normal from 1949 to 1953 inclusive while the net water balance was mostly deficient, yet an appreciable upward trend in growth took place during that time on Cape Breton Island.

Annual mortality (Fig. 8) does not show a clear relationship with the June to August net water balance. This is not surprising since many of the trees no doubt died during other times of the year. In fact at Fredericton, mortality appears to be inversely related to the June to August net water balance.

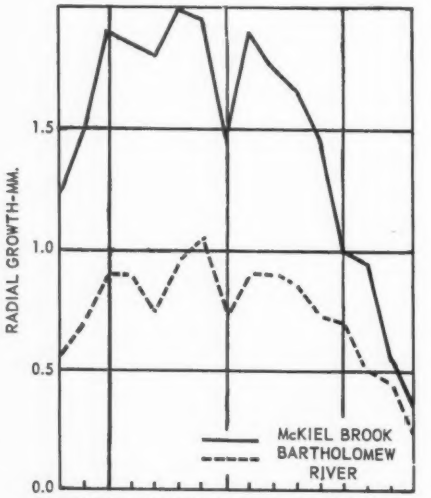

FIGURE 9. *Average radial growth of yellow birch in two stands, of different vigor, affected by dieback at the same time.*

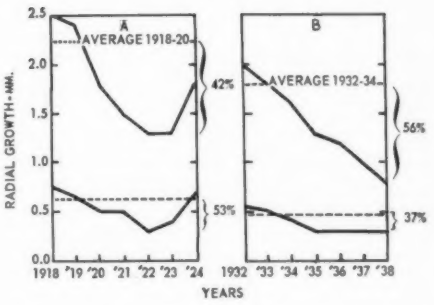

FIGURE 10. *Percentage growth reduction in high-vigor and low-vigor yellow birch trees (surviving dieback) during a period of subnormal precipitation (A) and during the early years of dieback (B).*

Discussion. The net water balance for the growing season gives a more realistic picture of complex moisture relations in the forest than the conventional sums of precipitation or averages of temperature can provide. The concept of evapo-transpiration as a function of field capacity deficiency (Thornthwaite and Hare, 1955) considers the soil moisture reserve to be only partly available to plants because withdrawal of moisture makes the remainder increasingly more difficult to remove. It acknowledges that a certain degree of drought occurs soon after soil moisture supplies begin to be used. Utilization of soil moisture in April and May therefore could result in a coetaneous deficiency that would make the usually inadequate rains of the June to August period the more severe (Tables 1 and 2). In the Maritime Provinces of Canada, a region that annually experiences a large autumn, winter, or spring water surplus, the growth of yellow birch has been closely related to the June to August net water balance both before and during dieback. However, the meteoro-

logical statistics fail to show that above normal need (due to high temperature) or subnormal supply (low rainfall) was directly responsible for the drastic reduction in growth which characterizes the early years of the disease.

Redmond (1957) found 90 percent of the feeding rootlets of yellow birch in the upper 5 cm. (including litter) of the soil. Aided by surface evaporation, such a concentration of absorbing rootlets might deplete the upper 2 inches of the forest floor below its field moisture capacity in April and May when replenishment of the internal moisture content of the tree is rapidly progressing (Clark and Gibbs, 1957). Such depletion of the soil water in the region of the feeding rootlets would create a potential stress on the moisture regime which, according to the present analysis of the water balance, might develop into a severe net deficiency during the June to August growing season. In a 4-year study of the moisture requirements of yellow birch Clark and Gibbs (1957) found that two water-deficient summers actually lowered the moisture content of twigs but they concluded, "there is no evidence that these or other water-deficient summers since 1897 might have been drastic enough to initiate the dieback of birch."

Braathe (1958) relates birch dieback to the March thaw of 1936. It has already been pointed out that Balch and Prebble (1940) dated the beginning of dieback in central New Brunswick at approximately 1932. Growth data in Figure 4 show that growth reduction, no doubt accompanied by advanced crown symptoms, definitely occurred in central New Brunswick in 1935. The approximate date of 1932 agrees with the evidence, whereas 1936 does not. On the basis of the apparent "uniformity" of dieback in 1956 (about a quarter of a century after the disease began) Braathe assumes that its initiation also must have been simultaneous and uniform, almost catastrophic. Published reports of the disease (Fig. 5) and other evidence presented in this paper clearly show that such was not the case.

Studies of climate and birch dieback in New Brunswick and Nova Scotia by Hawboldt (1952) and in the Province of Quebec by Pomerleau (1954) led these workers to the conclusion that the disease was a physiological disturbance brought about by a general warming up of the climate in eastern Canada since the early 1920's. Summer temperatures have increased 1.8° F. in Nova Scotia and 2.4° F. in New Brunswick (Hawboldt, 1952), and about 3° F. in the City of Quebec (Pomerleau, 1954). The implied inability of the trees to readjust to these small gradual changes is hard to explain in the light of Fraser's (1957) and Redmond's (1957) experimental results. During ecological studies on a yellow birch site at Chalk River, Ontario, Fraser noted that a "10-degree (F.) increase of soil temperature on the experimental plot in 1955 as compared with 1954, was not accompanied by a noticeable change in health of birch trees located thereon." By artificially raising the soil temperature 2° C. (3.6° F.) from June 3 to September 6, 1953, Redmond increased the mortality of yellow birch rootlets from 6 to 60 percent, but he stated, "on September 6 new rootlet development was found at a depth of six inches under an area where all roots two to three inches deep had been killed. Obviously the tree was attempting adjustment to the altered environment." Thus in only one growing season, and concurrently with elevated soil temperature, the trees made some progress in readjustment of their feeding rootlets to deeper levels. Redmond noted also that, "excavations made October 14 showed that new rootlets had begun already to develop in the soil where killing had occurred earlier because of heating." In other words, only five weeks after the artificially heated soil was allowed to return to its natural temperature, the trees were producing new feeding rootlets at the *same* depth as those which had been killed by heat a few months

earlier. In summation of his findings Redmond pointed out that, "in this case, initiation of the increase was abrupt and the roots had little chance to prepare defence against it through relocation as would have been possible if it had been brought about gradually."

Pomerleau (1949, 1953) claims that in the Province of Quebec dieback is not confined to birch but that it is prevalent also in other hardwood genera and even in some coniferous species. In the Maritime Provinces there has been no widespread deterioration and mortality of other species except that caused by the spruce budworm (*Choristoneura fumiferana* Clem.). The specific nature of birch dieback was early noted and illustrated by Balch and Prebble (1940, Fig. 3). Figure 11 illustrates the present healthy condition of other hardwoods in comparison with the almost complete devastation of birch in the same stand, a condition observable throughout the region.

Clark and Gibbs (1957) and Redmond (1957) have already noted the failure of the climatic change theory to fit the pattern of apparent spread of birch dieback (Fig. 4).

That there has been a warming up in the northern hemisphere, particularly north

FIGURE 11. *Aerial photograph of a hardwood forest in central New Brunswick taken on July 10, 1957. The remains of large yellow birch trees killed by dieback contrast with the healthy crowns of other hardwoods, mostly maple. (Photo. R. E. Balch.)*

of the 40th parallel, over the past few decades, is supported by much evidence (Shapley, 1953). However, if the birch deterioration was in the first instance the result of increasing temperature it is logical to expect the earliest deterioration would have appeared in the warmer areas of the yellow birch range, that is towards the southern and western boundaries. Similarly, any improvement in the condition of the trees due to relief from the heat stress, would be expected to appear first in the cooler areas of the tree's range, that is, in the Maritime Provinces and particularly near the coasts. Such expectations are not borne out by the reported occurrence of and recovery from the disease.

The dissimilar growth behavior of high vigor and low vigor trees during drought and dieback further detracts from the climatic theory. The greater growth reduction of the more vigorous trees during dieback is an interesting feature of the dissimilarity. A possible explanation is found in a statement by Bawden (1950, p. 34) describing the reaction of plants to viruses: "Almost invariably, the more vigorously a plant is growing at the time of infection, the more pronounced will be the symptoms and the more generally will they occur over systemically infected plants." On the basis of Bawden's statement the data presented here on the growth behavior of vigorous yellow birch trees, seem to support Berbee's (1957) observation that "many of these (dieback) symptoms seemed to be typical of virus diseases." If a virus is responsible for dieback, the actual evapotranspiration or the availability of soil moisture might be among the most important regulators of the condition of the material on which the virus depends for its activity.

Summary and Conclusions

1. Studies of the radial growth of yellow birch at different levels in the tree show that growth reduction due to dieback was simultaneous throughout the tree. This justified the use of growth at breast height as a measure of growth behavior of the tree.
2. Studies of the seasonal growth of yellow birch show that 90 percent or more of the total radial increment takes place during June to August inclusive.
3. The growth curves of yellow birch and sugar maple behaved similarly until the commencement of dieback, when the growth of birch was drastically reduced for a lengthy period while that of the maple fluctuated normally. The points of divergence of birch and maple growth curves are used as a means of dating birch dieback.
4. The growth of birch in the Maritime Provinces of Canada, before the onset and during the course of dieback, is related to the June to August net water balance. High temperature and low rainfall in April and May bring about early seasonal utilization of the soil moisture reserve, thus making the usually inadequate precipitation of the June to August period the more severe. This important effect of the distribution of precipitation is not allowed for in analyses based on total precipitation.
5. The growth reactions of yellow birch trees during drought and when affected by dieback are different. During a period of drought in the early 1920's high vigor trees showed 42 percent growth reduction as compared with 53 percent for low vigor trees; during the early years of dieback the percentages were 56 and 37 respectively.
6. Growth trends of yellow birch in different areas lead to the conclusion that dieback actually spread from central New Brunswick. This conclusion is supported by mortality

data and by the published reports on the occurrence of the disease.

7. Analyses of climatic data according to Thornthwaite's water balance technique have revealed a more realistic basis of evaluating the effect of climate on the growth of yellow birch than the conventional sums of precipitation or averages of temperature can provide. The water balance variations and the fact that growth reduction was greatest in vigorous trees cannot be reconciled with the hypothesis that dieback is a purely physiological disturbance brought about by climatic stress; nor is there a coherent theorem of the mechanism by which the suggested physiological disturbance is related to climatic factors. Instead, these facts, together with our evidence of spread and Berbee's description of typical virus symptoms, suggest that birch dieback is an infectious disease.

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